
Volume 95
Number 4
2008

MISSOURI BOTANICAL
JAN 21 2009
GARDEN LIBRARY

Annals
of the
Missouri
Botanical
Garden



CHROMOSOME NUMBERS IN
VERONICEAE (PLANTAGINACEAE):
REVIEW AND SEVERAL NEW
COUNTS¹

D. C. Albach,² M. M. Martínez-Ortega,³
L. Delgado,³ H. Weiss-Schneeweiss,⁴
F. Özgökce,⁵ and M. A. Fischer¹

ABSTRACT

Chromosomal evolution in *Veronica* L. and related genera (*Wulfenia* Jacq., *Wulfeniopsis* D. Y. Hong, *Paederota* L., *Lagotis* Gaertn., *Picrorhiza* Royle ex Benth., and *Veronicastrum* Heist. ex Fabr.; Veroniceae, Plantaginaceae; formerly Scrophulariaceae) is presented. To this end, we conducted an extensive literature survey of more than 400 publications covering ca. 300 out of 500 species in the tribe. We also report 44 new chromosome counts. Chromosome numbers of *Veronica hispidula* Boiss. & Huet. ($2n = 18, 36$) and *V. reuteriana* Boiss. ($2n = 28, 42$) are reported for the first time, and both species exhibit intraspecific ploidy level variation. Other new counts confirm chromosome numbers reported previously. The evolution of chromosome numbers in Veroniceae is discussed in light of recent results from DNA-based phylogenetic analyses. Most of the subgenera of *Veronica* exhibit only one single basic number, i.e., $x = 6, 7, 8, 9, 12, 17$, or $20/21$. In this genus, the putative ancestral base number of 9 has been reduced several times to 8 and 7, respectively (aneuploidy/dysploidy), often associated with transition to annual life history. In contrast, no unambiguous increase of chromosome base number has been inferred. A table that includes all species of Veroniceae and, if known, their chromosome number and full sectional and subsectional classification in *Veronica* is provided. For this purpose, three new combinations have been introduced (*Veronica* sect. *Acinifolia* (Römpf) Albach, *Veronica* sect. *Glandulosae* (Römpf) Albach, and *Veronica* subsect. *Cochlidiosperma* (Rechb.) Albach).

Key words: Annual habit, chromosome numbers, dysploidy, Plantaginaceae, polyploidy, *Veronica*, Veroniceae.

The tribe Veroniceae within the Plantaginaceae (sensu Angiosperm Phylogeny Group, 2003; formerly part of Scrophulariaceae) comprises about 500 species

distributed mainly in temperate regions of the Northern Hemisphere and Australasia. By far, the largest genus in the tribe is *Veronica* L., with ca. 450

¹ We thank the Austrian Science Foundation (FWF) project P-15336 for funding research by DCA. The input of MIMO and LD was partly supported by the Junta de Castilla y León through the research project SA048A05 and partly by the project Flora Iberica VI (REN2002-04634-C05-02). Help from K. Marlowe and V. Vladimirov in getting literature, translations by Y.-P. Guo and S. von Mehring, and loan of voucher specimens by the curators of G, M, MSB, L. U, NCU, and NEU are also gratefully acknowledged. We also thank colleagues who have helped collect material for this study.

² Institut für Spezielle Botanik und Botanischer Garten, Johannes Gutenberg-Universität Mainz, Bentzelweg 9b, 55099 Mainz, Germany. albach@uni-mainz.de.

³ Departamento de Botánica, Universidad de Salamanca, E-37007 Salamanca, Spain. mmo@usal.es; ldelsan@usal.es.

⁴ Department of Systematic and Evolutionary Botany, Faculty Center Botany, Universität Wien, Rennweg 14, 1030 Wien, Austria. hanna.schneeweiss@univie.ac.at; manfred.a.fischer@univie.ac.at.

⁵ Department of Biology, Faculty of Science and Arts, Yüzüncü Yıl University, 65080 Van, Turkey.
doi: 10.3417/2006094

species, which has recently been recircumscribed to include (again) the Australasian species of the *Hebe* complex (Albach et al., 2004b; Garnock-Jones et al., 2007). Growing information on phylogenetic relationships in the tribe (e.g., Albach & Chase, 2001, 2004; Albach et al., 2004a, c) has highlighted the need to summarize available information for characters important for the evolution of the tribe and to point out critical taxa for which this character has not yet been investigated. One of these characters is chromosome number. Since the first publication of chromosome numbers in *Veronica* by Heitz (1926), many authors have published chromosome numbers, including some extensive regional surveys (e.g., Iceland, Löve & Löve, 1956; Belarus, Dzhus & Dmitrieva, 2001) and other extensive surveys of smaller groups within *Veronica* (e.g., subsection *Acinifolia* (Römpf) Stroh; Fischer, 1972). Albach et al. (2004a) gave the first overview of the evolution of chromosome numbers in Veroniceae. The principal result was that $x = 9$ is the ancestral chromosome number in *Veronica*, with just one reduction to $x = 8$ but four independent reductions to $x = 7$ (once from $x = 8$, but three times from $x = 9$) (Albach et al., 2004a). Dysploidy is, in most cases, associated with a transition to annual life history (Albach et al., 2004a). Here, we investigate the evolution of chromosome numbers of Veroniceae in more detail and highlight those species or populations that need further investigation. Evolutionary relationships detected in major contributions to floras (e.g., Turkey and Iran, Fischer, 1978, 1981; China, Hong & Fischer, 1998; Spain, Martínez-Ortega et al., in press) combined with results from molecular systematic analyses (e.g., Albach et al., 2004a) form the basis of the discussion.

The present contribution is based on previously published chromosome numbers, but also includes 44 new reports of chromosome numbers. This review presents a first attempt to survey all chromosome numbers worldwide for the entire tribe Veroniceae, and although we are aware that our list is not yet complete, we hope that this review will allow some evolutionary conclusions and also stimulate chromosome studies of those species that are the most interesting but not yet counted. Finally, we want to strongly emphasize the great need for good quality figures accompanying the publication of any new chromosome numbers and the necessity to provide voucher information for each count.

MATERIALS AND METHODS

We have found more than 400 publications including chromosome numbers in Veroniceae representing more than 2600 populations. Several comprehensive reviews of chromosome numbers for regional

floras (e.g., the former Soviet Union, Agapova et al., 1993; Austria, Dobeš & Vitek, 2000) as well as worldwide (e.g., Goldblatt & Johnson, 2006) do exist and greatly facilitated this work. Concomitantly, frequent errors have been encountered in these surveys. Whenever feasible, we checked the original source, and eventually we checked ca. 350 original publications (including ca. 2500 studied populations within the Veroniceae).

Here, we use the supraspecific classification of Albach et al. (2004b) and the species in Veroniceae currently accepted by us (Albach, Martínez-Ortega & Fischer, unpublished data). Author names of taxa are given in Appendix 1. Original chromosome counts were conducted mostly using seeds collected in the field and germinated in the laboratory. For *Veronica bellidioides* L., actively growing root tips of plants cultivated in the Botanical Garden of the University of Vienna (Austria) were used. Root tips were pretreated with 0.002 M 8-hydroxyquinoline for 2 hr. at room temperature and 1.5 hr. at 4 °C, and fixed in 3 ethanol:1 acetic acid for 24 hr. at room temperature and stored at –20 °C or 4 °C until use. For *V. persica* Poir. as well as other taxa studied by LD and MMO, flower buds were collected in the field and fixed in modified Carnoy's solution (4 chloroform:3 absolute ethanol:1 glacial acetic acid), transferred to 70% ethanol, and stored at 4 °C until use. For chromosome counts by HWS and DCA, material was hydrolyzed in 5N HCl for 20 min., washed, and Feulgen-stained in Schiff's reagent (Fukui & Nakayama, 1996) for 1–1.5 hr. in the dark. Material analyzed by MMO and LD was stained in 2% acetic orcein (La Cour, 1954). All squash preparations were made in a drop of 45% acetic acid. Chromosome numbers were analyzed under light microscopy (Carl Zeiss AG, Oberkochen, Germany) by HWS and DCA or Nikon Optiphot (Nikon Corp., Tokyo, Japan) by MMO and LD and documented with black-and-white photography (Fig. 1). For each individual, several cells (a minimum of five) with well-spread chromosomes were used for chromosome number determination. Chromosome counts by MAF followed the methods given in Fischer (1975a). Vouchers from DCA and MAF were deposited in the herbarium of the University of Vienna (WU) and those from MMO and LD at the University of Salamanca (SALA).

In an electronic appendix (available at <http://www.spezbol.fbl10.uni-mainz.de/home_e/img/albach_appendix.xls>), we have summarized ca. 2600 chromosome counts from ca. 400 publications. Both haploid and diploid counts were considered. The original plant name under which the count was published as well as the currently accepted name are given.

To test whether chromosome number (n , $2n$), chromosome base number (x), and ploidy levels significantly differ between annuals and perennials, the Mann-Whitney U test has been used. To avoid an overly large influence from the large radiation of Australasian species in the *Veronica*, which are likely of hexaploid origin with respect to other *Veronica*, statistical comparisons were conducted with and without Australasian species as well as those species with $x = 17$ (*Veronicastrum* Heist. ex Fabr., *Picrorhiza* Royle ex Benth., *Veronica* subg. *Pseudolysimachium* (Opiz) Buchenau).

RESULTS AND DISCUSSION

Forty-four chromosome counts reported here for the first time are summarized in Table 1, and for 13 significant reports, photographs are presented (Fig. 1). Currently, chromosome numbers for 330 of 509 species (65%) in Veroniceae have been published (Appendix 1, see electronic appendix for a comprehensive listing at <http://www.spezbot.fb10.uni-mainz.de/home_e/img/albach_appendix.xls>). However, some groups are well known (e.g., *Veronica* subg. *Cochlidiosperma* (Rchb.) M. M. Mart. Ort. & Albach and *Veronica* subg. *Synthyris* (Benth.) M. M. Mart. Ort., Albach & M. A. Fisch.—all known species have been counted), whereas other groups include many species for which no count is available. Most notably, chromosome numbers of less than one fourth (23%) of the species of *Lagotis* Gaertn. and only about one third (32%) of the species of *Veronica* subg. *Stenocarpon* (Boriss.) M. M. Mart. Ort., Albach & M. A. Fisch. are known. Chromosome base numbers (Table 2) and ploidy levels (Table 3) have been summarized, arranged by subgenus in *Veronica*. Albach et al. (2004a) discussed the ancestral chromosome number in Veroniceae, which is inferred to be $x = 9$, although $x = 5$ is also possible (Lepper, 1964; Albach & Chase, 2004). They further inferred a single origin of $x = 8$ within *Veronica* (the $x = 8$ clade). However, a more detailed analysis shows that independent origins of $x = 8$ occurred in several instances independently (Fig. 2; see below). Albach et al. (2004a) also reported four independent changes to $x = 7$ (Fig. 2), which now needs to be revised to six changes (two from $x = 9$, three from $x = 8$, one ambiguous optimization) because of overlooked numbers in *V. densiflora* Ledeb. (*Veronica* subg. *Stenocarpon*) and *V. magna* M. A. Fisch. (*Veronica* subg. *Chamaedrys* (W. D. J. Koch) Buchenau). No unambiguous chromosome number increases between $x = 7$, 8, and 9 are inferred (Albach et al., 2004a; and updated by information presented here).

The evolution of an annual life history in *Veronica* has been studied in various aspects in recent years.

Molecular phylogenetic analyses have shown that an annual life history arose several times independently (Albach et al., 2004c). Analyzing genome size in *Veronica* has demonstrated that a low genome size is correlated with selfing rather than with annual life history (Albach & Greilhuber, 2004) as previously suggested (Bennett, 1972). A higher DNA substitution rate, however, is not correlated with selfing, but rather with an annual life history in *Veronica* (Albach & Müller, in prep.), supporting more general results for all angiosperms (Bousquet et al., 1992). Therefore, it seems appropriate to analyze whether chromosome numbers differ between annuals and perennials. Several studies (e.g., Levin, 2002) have suggested a reduction in chromosome number associated with the shift from perennial to annual life history. Standard statistics are not as powerful as statistical methods incorporating phylogenetic evidence due to the confounding effect of shared evolutionary history on the results (Harvey & Rambaut, 1998). However, a fully resolved phylogeny for all species of Veroniceae for which chromosome numbers are available does not exist and is not even possible to generate due to the reticulate history especially of polyploid taxa (e.g., Albach, 2007). The results of the statistical analysis nevertheless appear robust in showing annual species to have a significantly lower chromosome base number but not a lower ploidy level. The inclusion of Australasian species of *Veronica* and those species with $x = 17$ (*Veronicastrum*, *Picrorhiza*, *Veronica* subg. *Pseudolysimachium*) in an analysis has the effect that annual species have a significantly lower chromosome number and ploidy level. Without those perennial species, annual species have on average a ploidy level of 3.3, whereas perennial species have a ploidy level of 3.4, which is not significantly different ($P = 0.85$). Chromosome base numbers, however, differ significantly, with a lower number found in annuals ($P < 0.01$). We could not check whether this is an indirect effect of a correlation of selfing with a lower chromosome base number, as is the case in the evolution of genome size (Albach & Greilhuber, 2004), due to the paucity of information on breeding systems in the Veroniceae. Both reduction in chromosome number and selfing may reduce recombination rates and, therefore, it appears likely that both are selected for instances in which a low recombination rate is advantageous. The chromosome number is the product of ploidy level and chromosome base number, and its distribution is not significantly different ($P = 0.19$) within the Veroniceae.

VERONICEAE EXCLUDING VERONICA

Veroniceae in the circumscription of Albach et al. (2004b) comprise nine genera, including two mono-

Table 1. Information on chromosome counts in *Veronica* reported here for the first time. Counts performed by DCA, HWS, LD, MAF, and MMO.

Species	Chromosome number	Counted by	Origin	Voucher
<i>V. alpina</i> L.	2n = 18	LD, MMO	Spain, Huesca: Torla, Bujaruelo, N face of Pico Gabieto	<i>M. M. Martínez-Ortega 300</i> (SALA)
<i>V. alpina</i>	2n = 18	LD, MMO	Spain, Huesca: Benasque, La Renclusa, 7 Aug. 1997	<i>M. M. Martínez-Ortega s.n.</i> (SALA)
<i>V. anagalloides</i> subsp. <i>heureka</i> M. A. Fisch.	2n = 18	HWS, DCA	Georgia, Greater Caucasus: Cross Pass	<i>D. C. Albach 299</i> (WU)
<i>V. aphylla</i> L.	n = 9, 2n = 18	LD, MMO	Spain, Navarra: Isaba, Portillo de Arrasarguiat	<i>L. Delgado 337</i> (SALA 110613)
<i>V. arguteserrata</i> Regel & Schmalh.	2n = 42, Fig. 1A	HWS, DCA	Turkey, Bitlis: Murat valley betw. Hamur and Tutak	<i>D. C. Albach 685</i> (WU)
<i>V. bellidioides</i> L.	2n = 36	HWS, DCA	Bulgaria, Mt. Pirin	<i>D. C. Albach 551</i> (WU)
<i>V. bellidioides</i>	2n = 36	HWS	Spain, Pyrenees	<i>P. Schönswetter 148/21</i> (WU)
<i>V. bombycina</i> Boiss. & Kotschy subsp. <i>bombycina</i>	2n = 16	MAF	Cult. Bot. Gard. Vienna, 13 May 1969	<i>M. A. Fischer s.n.</i> (WU)
<i>V. bozakmanii</i> M. A. Fisch.	2n = 28	HWS, DCA	Turkey, Bitlis: Kucuksu	<i>D. C. Albach 611</i> (WU)
<i>V. bozakmanii</i>	2n = 28, Fig. 1B	HWS, DCA	Turkey, Bitlis: W of Kuzgunkegan Pass	<i>D. C. Albach 667</i> (WU)
<i>V. campylopoda</i> Boiss.	2n = 42, Fig. 1C	DCA	Turkey, Van: W of Güzeldere Pass	<i>D. C. Albach 653</i> (WU)
<i>V. campylopoda</i>	2n = 56, Fig. 1D	DCA	Turkey, Van: Catak (cultivated at Technical University of Denmark, Lyngby)	<i>Jensen IOK-6/2003</i> (WU)
<i>V. chamaedrys</i> L. subsp. <i>chamaedrys</i>	2n = 32	LD, MMO	Spain, Oviedo: Quirós, toward Pico Gamoniteiro	<i>L. Delgado 768 & E. Rico</i> (SALA 110656)
<i>V. chamaedrys</i> subsp. <i>chamaedrys</i>	2n = 32	LD, MMO	Spain, Teruel: from Fontanete to Valdelinares	<i>E. Rico 7078</i> (SALA 110655)
<i>V. ciliata</i> subsp. <i>cephaloides</i> (Pennell) D. Y. Hong	2n = 16, Fig. 1K	HWS, DCA	China, Xizang (Tibet)	<i>G. Miede 98-16717</i> (GOET)
<i>V. cymbalaria</i> Bodard	2n = 36	MAF	Greece, Crete, Omalos: Xyloskalon, 6 May 1971	<i>H. Malicky s.n.</i> (WU)
<i>V. cymbalaria</i>	2n = 36	MAF	Greece, Crete, Ida mtns.: near Ideon Antron cave, 9 May 1971	<i>H. Malicky s.n.</i> (WU)
<i>V. cymbalaria</i>	2n = 54	MAF	Greece, Ionian Islands, Kefallinia: area betw. Sami & Dhihalia, 11 Apr. 1974	<i>M. & G. Fischer s.n.</i> (WU)
<i>V. cymbalaria</i>	2n = 54	MAF	Greece, Ionian Islands, Kefallinia: Mt. Rudi, 13 Apr. 1974	<i>M. & G. Fischer s.n.</i> (WU)
<i>V. cymbalaria</i>	2n = 54	MAF	Greece, Ionian Islands, Kefallinia: area betw. Sami & Dhihalia, 14 Apr. 1974	<i>M. & G. Fischer s.n.</i> (WU)
<i>V. filiformis</i> Sm.	2n = 14	Tanja Lessel, DCA	Austria, Graz: Schubertstrasse, in front of Botanical Garden	<i>D. C. Albach 857</i> (MJG)
<i>V. fruticans</i> subsp. <i>cantabrica</i> M. Laínz	n = 8, 2n = 16	LD, MMO	Spain, Cantabria: Hermandad de Campoo de Suso, base of Pico Tres Mares, 11 July 1996	<i>M. M. Martínez-Ortega s.n.</i> (SALA)
<i>V. fruticans</i> subsp. <i>cantabrica</i>	2n = 16	LD, MMO	Spain, Segovia: El Cardoso de la Sierra, Pico del Lobo, 2 July 1996	<i>M. M. Martínez-Ortega s.n.</i> (SALA)
<i>V. fruticans</i> subsp. <i>cantabrica</i>	2n = 16	LD, MMO	Spain, La Rioja: Canales de la Sierra, Pico Gatón	<i>M. M. Martínez-Ortega s.n.</i> (SALA)

Table 1. Continued.

Species	Chromosome number	Counted by	Origin	Voucher
<i>V. fruticans</i> subsp. <i>cantabrica</i>	$2n = 16$	LD, MMO	Spain. Ávila: Solana de Ávila, Lagunas de El Trampal, N slope	<i>E. Rico</i> 7105 (SALA 110610)
<i>V. fruticans</i> subsp. <i>cantabrica</i>	$2n = 16$	LD, MMO	Spain. Lérida: Pla de Beret	<i>L. Delgado</i> 344 & <i>I. Soriano</i> (SALA 110609)
<i>V. gentianoides</i> Vahl	$2n = \text{ca. } 72$	DCA	Georgia. Greater Caucasus: W of Truso Gorge	<i>D. C. Albach</i> 350 (WU)
<i>V. gentianoides</i>	$2n = 36$, Fig. 1I	HWS, DCA	Georgia. Greater Caucasus: meadows above Zaminda Sameba	<i>D. C. Albach</i> 341 (WU)
<i>V. gentianoides</i>	$2n = \text{ca. } 72$	DCA	Georgia. Greater Caucasus: beech forest below Zaminda Sameba	<i>D. C. Albach</i> 318 (WU)
<i>V. gentianoides</i>	$2n = 46\text{--}48$, Fig. 1H	DCA	Georgia. Greater Caucasus: below Dzuta	<i>D. C. Albach</i> 333 (WU)
<i>V. hispidula</i> Boiss. & Huet.	$2n = 18$ (5 seedlings), Fig. 1E; $2n = 36$ (1 seedling) Fig. 1G	HWS, DCA	Turkey. Van: Degitmenköy	<i>D. C. Albach</i> 635 (WU)
<i>V. micrantha</i> Hoffmans. & Link	$n = 8$, $2n = 16$, Fig. 1M	LD, MMO	Spain. Salamanca: Peñaparda, Mostejal brook	<i>L. Delgado</i> 34, <i>X. Giráldez</i> & <i>E. Rico</i> 16-VI-1998 (SALA 110657)
<i>V. nummularia</i> Gouan	$2n = 16$, Fig. 1J	LD, MMO	Spain. Huesca: Ansó, Collado de Petrachema, N side	<i>L. Delgado</i> 332 & <i>I. Soriano</i> 25-VI-2000 (SALA 110612)
<i>V. peduncularis</i> M. Bieb.	$2n = 16\text{--}18$	DCA	Georgia. Greater Caucasus: Kazbegi	<i>D. C. Albach</i> 325 (WU)
<i>V. persica</i> Poir.	$2n = 28$	HWS	Azerbaijan. Talysh: forest reserve Qirkan qorugu, SW of Lankaran	<i>G. Schneeweiss</i> Geo01 132/28 (WU)
<i>V. ponae</i> Gouan	$2n = 54$	LD, MMO	Spain. Huesca: Panticosa, toward lakes	<i>M. Santos Vicente</i> 455, <i>L. P. Gavilán Iglesias</i> & <i>L. M^a. Muñoz Centeno</i> (SALA 110608)
<i>V. prostrata</i> L.	$2n = 16$	LD, MMO	Czech Republic. Beroun	<i>M. M. Martínez-Ortega</i> 1331 (SALA)
<i>V. reuteriana</i> Boiss.	$2n = 28$, Fig. 1L	HWS, DCA	Turkey. Van: Catak	<i>D. C. Albach</i> 691 (WU)
<i>V. reuteriana</i>	$2n = 42$, Fig. 1F	HWS, DCA	Turkey. Bitlis: S of Tutak	<i>D. C. Albach</i> 676 (WU)
<i>V. scheereri</i> (J. P. Brandt) Holub	$2n = 32$	LD, MMO	Spain. Huesca: Ansó, on the way to Collado de Petrachema	<i>L. Delgado</i> 328 & <i>I. Soriano</i> (SALA 110643)
<i>V. scheereri</i>	$2n = 32$	LD, MMO	Germany. Baden-Württemberg: Schwäbische Alb	<i>M. M. Martínez-Ortega</i> 1093 (SALA)
<i>V. scutellata</i> L.	$2n = 18$	LD, MMO	Spain. Salamanca: Fuenteguinaldo, meadows of El Potril, banks of Río Agueda, 17 June 1996	<i>M. M. Martínez-Ortega</i> s.n. & <i>E. Rico</i> (SALA)
<i>V.</i> sp. indet., aff. <i>beccabungoides</i>	$2n = 36$	HWS, DCA	Georgia. Greater Caucasus: Kazbegi	<i>D. C. Albach</i> 329 (WU)
<i>V. trichadena</i> Jord. & Fourr.	$2n = 36$	MAF	Turkey. Mugla: Sakar pass, ca. 15 km S of Mugla, 28 Mar. 1978	<i>G. & M. A. Fischer</i> s.n. (WU)

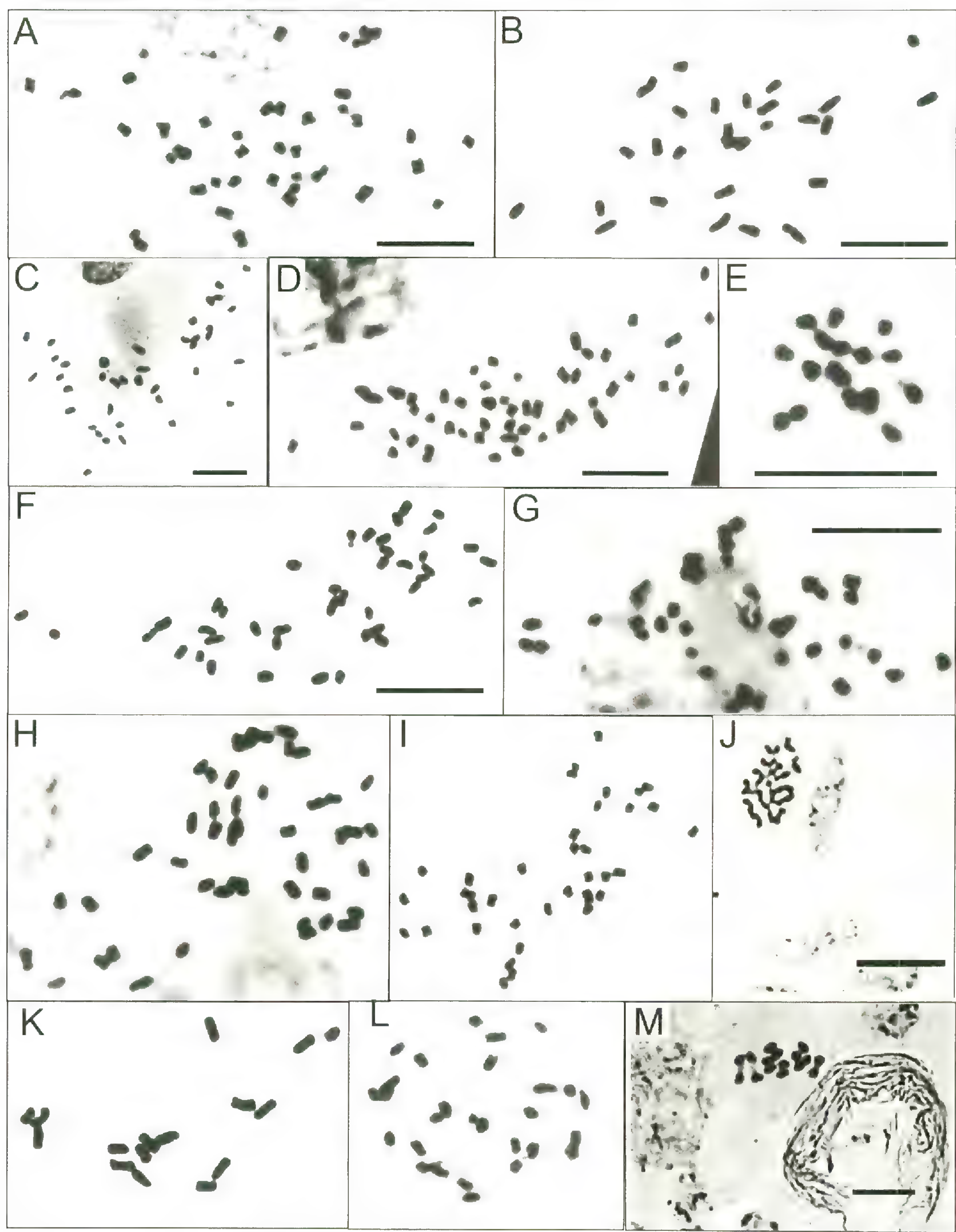


Figure 1. Photos of chromosome counts. Scale bars = 10 μ m. —A. *Veronica arguteserrata* (Albach 685, WU). —B. *V. bozakmanii* (Albach 667, WU). —C. *V. campylopoda* (Albach 653, WU). —D. *V. campylopoda* (Jensen IOK-6/2003, WU). —E. *V. hispidula* (Albach 635, WU). —F. *V. reuteriana* (Albach 676, WU). —G. *V. hispidula* (Albach 635, WU). —H. *V. gentianoides* (Albach 333, WU). —I. *V. gentianoides* (Albach 341, WU). —J. *V. nummularia* (Delgado 332, SALA). —K. *V. ciliata* subsp. *cephaloides* (Miehe 98-16717, GOET). —L. *V. reuteriana* (Albach 691, WU). —M. *V. micrantha* (Delgado 34, SALA).

Table 2. Chromosome base number for species arranged according to major clades in Veroniceae. Ancestral character state for each clade is underlined, based on information given in Albach et al. (2004a) and Wagstaff and Garnock-Jones (1998).

	$x = 7$	$x = 8$	$x = 9$	$x = 17$	$x = 20$	$x = 21$	$x = \text{other}$	Unknown
Veroniceae excluding <i>Veronica</i>		2	<u>6</u>	6			7	40
<i>Veronica</i> subgen. <i>Veronica</i>	2	3	<u>19</u>				1	20
Subg. <i>Beccabunga</i>	8	2	<u>13</u>					10
Subg. <i>Pseudolysimachium</i>				<u>18</u>				11
Subg. <i>Synthyris</i>							<u>18</u>	
Subg. <i>Cochlidiosperma</i>			<u>10</u>				<u>1</u>	1
Subg. <i>Pellidosperma</i>	1	1	<u>2</u>					3
Subg. <i>Stenocarpon</i>		<u>11</u>						22
Subg. <i>Pocilla</i>	<u>14</u>							14
Subg. <i>Pentasepalae</i>		<u>33</u>						37
Subg. <i>Chamaedrys</i>	1	<u>11</u>						1
Sect. <i>Derwentia</i>				1	4	<u>4</u>	11	3
Sect. <i>Hebe</i>					69	<u>46</u>	3	16
Other species of <i>Veronica</i>		1					2	—
Total (out of 509 species)	26	64	50	25	73	50	43	178

typic ones for which no chromosome numbers are known (*Scrofella* Maxim. from China, *Kashmiria* D. Y. Hong from the Himalayas).

Lagotis is the least studied group in Veroniceae despite its wide occurrence from eastern Turkey to Alaska. Although 35 chromosome numbers are available, only seven of 31 species in the genus have been studied. All reported chromosome numbers are based on $x = 11$, except for $2n = 54$ for *L. brevituba* Maxim. (Huang et al., 1996). Unfortunately, no figure is included in the latter publication and, therefore, this number requires confirmation. *Lagotis stolonifera* (K. Koch) Maxim. (two counts), *L. takedana* Miyabe & Tatew. (one count), *L. cashmeriana* (Royle) Rupr. (three counts), and *L. glauca* Gaertn. (five counts) are diploids ($2n = 2x = 22$), whereas *L. integrifolia* (Willd.) Schischk. (three counts) is tetraploid ($2n = 4x = 44$). *Lagotis minor* (Willd.) Standl. has been studied intensively (16 counts), with more than half (nine counts) being tetraploid ($2n = 2x = 44$) and the rest diploid ($2n = 2x = 22$). Most of the counts for *L. minor* are from Russia, with only one diploid count from Canada. The taxonomic concept of *L. minor* and related species is complex, and confusion with *L.*

Table 3. Occurrence of polyploidy in various taxa of Veroniceae and among annual and perennial species of the tribe. In the line labeled “Perennial species,” note that Australasian taxa and those with $x = 17$ have been excluded.

	$2x$	$4x$	$6x$	$8x$	$10x$	$12x$	$16x/18x$
Non- <i>Veronica</i> Veroniceae	10	10	1	1			1
Subg. <i>Veronica</i>	14	6	6	1			
Subg. <i>Beccabunga</i>	13	14	5	1	1		
Subg. <i>Pseudolysimachium</i>		16		9			
Subg. <i>Synthyris</i>	16	5					
Subg. <i>Cochlidiosperma</i>	7	3	2				
Subg. <i>Pellidosperma</i>	4						
Subg. <i>Stenocarpon</i>	10	1					
Subg. <i>Pocilla</i>	6	7	3	1			
Subg. <i>Pentasepalae</i>	22	7	5	6	2		
Subg. <i>Chamaedrys</i>	10	2	1				
Sect. <i>Derwentia</i>			15			5	
Sect. <i>Hebe</i>			87			26	15
Others	2	1					
Total	117	68	118	8	4	26	16
Annual species	30	16	8	1			
Perennial species	86	35	15	8	3		
All perennial species	86	56	117	18	3	31	16

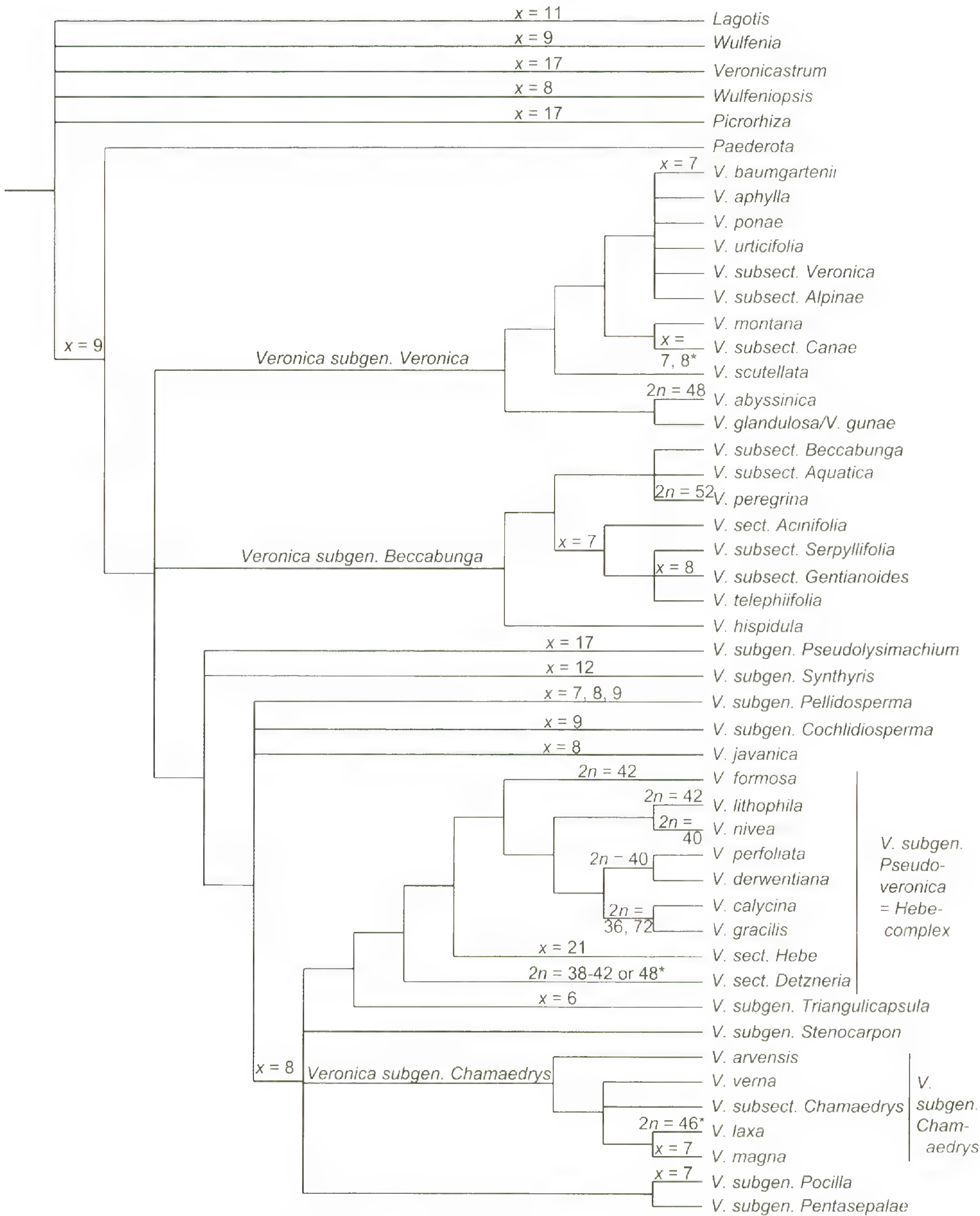


Figure 2. Cladogram showing the relationships of Veroniceae based on information from Albach et al. (2004a, c; 2005a, b; Albach, unpublished data). Asterisks mark counts that are considered dubious (see text for details).

glauca in the east and *L. integrifolia* in the south of the distribution is likely (Hultén, 1930). Unfortunately, voucher specimens for many counts are not cited clearly. A detailed analysis using morphological, karyological, and molecular methods would, therefore, be necessary to disentangle the taxonomic problems around *L. minor*.

Wulfenia Jacq. (from the southeastern Alps, western Balkan Peninsula, and southern Turkey) and *Paederota* L. (from the southeastern Alps) have $x = 9$, with *Wulfenia* being diploid ($2n = 2x = 18$; *W. carinthiaca* Jacq., *W. bleicicii* Lakušić, *W. orientalis* Boiss., and *W. baldacii* Degen with the first counted 11 times, and the latter three counted just once each) and *Paederota*

being tetraploid ($2n = 4x = 36$), although a single hexaploid plant of *P. lutea* Scop. ($2n = 6x = 54$) was found by Fischer (1969).

Wulfeniopsis D. Y. Hong (from Afghanistan to Nepal) includes two species that were both reported mostly as diploids ($2n = 2x = 16$) based on $x = 8$ (*W. amherstiana* (Benth.) D. Y. Hong, 11 counts; *W. nepalensis* (T. Yamaz.) D. Y. Hong, 1 count), with only one plant being tetraploid ($2n = 4x = 32$; *W. amherstiana*). *Veronicastrum* (from eastern Asia) and *Picrorhiza* (from the Himalayas) have been demonstrated to be tetraploid hybrids of *Wulfeniopsis* with *Wulfenia* and the common progenitor of *Veronica* plus *Paederota*, respectively (Albach & Chase, 2004). Therefore, $2x_{pic}$ and $2x_{vst}$ are $4x$ with respect to the rest of the tribe. Chromosome numbers are only available for one of three species of *Picrorhiza* (*P. kurrooa* Royle ex Benth, single count; $2n = 2x_{pic} = 34$) and six of 18 species of *Veronicastrum*, with *V. sibiricum* (L.) Pennell (7 counts), *V. virginicum* Farw. (3 counts), *V. brunonianum* (Benth.) D. Y. Hong, and *V. japonicum* (Nakai) T. Yamaz. (both counted once) being diploid ($2n = 2x_{vst} = 34$), *V. villosulum* (Miq.) T. Yamaz. tetraploid ($2n = 4x_{vst} = 68$; one count), and *V. liukiense* (Ohwi) T. Yamaz. octoploid ($2n = 8x_{vst} = 136$; one count) based on $x = 17$, which is the sum of the chromosome numbers of their inferred parents ($x_{pic}/x_{vst} = 8 + 9$).

Veronica s.l., according to Albach et al. (2004b) and Garnock-Jones et al. (2007), consists of 12 subgenera.

1. VERONICA SUBG. VERONICA

Veronica subg. *Veronica* includes 45 species with chromosome numbers available for 25 (Appendix 1). Molecular systematic analyses (Albach & Chase, 2001; Albach et al., 2004a, b) have identified an early branching clade that includes the African species of *Veronica*, as well as *V. scutellata* L., and a group of montane to subalpine Chinese–Himalayan species plus *V. montana* L. as consecutive sisters to a crown group of montane to subalpine species from the Northern Hemisphere including the type species *V. officinalis* L. (within subsection *Veronica*, Fig. 2). African species are characterized by high chromosome numbers. The two closely related species *V. glandulosa* Hochst. ex Benth. and *V. gunae* Schweinf. ex Engl. are both hexaploid ($2n = 6x = 54$) based on $x = 9$ (the most common base number in the group; two counts each), although only the extreme western populations of *V. glandulosa* from Cameroon, corresponding to subspecies *mannii* (Hook. f.) Elenevsky, have been counted. The annual *V. abyssinica* Fresen. also seems to be hexaploid ($2n = 6x = 48$; one count) based on $x = 8$; however, the number is based on only

one report. Clearly, more analyses for this species are desirable. Chromosome numbers of *V. scutellata* have been investigated from 27 localities throughout its entire distribution range in the northern parts of the Northern Hemisphere. All counts demonstrate that it is a diploid species ($2n = 2x = 18$).

The third section in subgenus *Veronica*, *Veronica* sect. *Montanae* (Boriss. ex Elenevsky) Assejeva, includes a group of Chinese–Himalayan species and *V. montana*, with the latter as sister to the rest (Albach, unpublished data). *Veronica montana* is diploid ($2n = 2x = 18$; 10 counts) almost throughout its distribution in Europe, with only a single tetraploid ($2n = 4x = 36$) found in France (Seidenbinder & Verlaque in Löve, 1985). The Chinese–Himalayan group in section *Montanae* is very poorly investigated. Only four of more than 20 species of subsection *Canae* (T. Yamaz.) Elenevsky have been investigated for chromosome numbers, and no clear pattern is present. A base chromosome number reduction to $x = 8$ seems to have occurred in *V. henryi* T. Yamaz. (tetraploid, $2n = 4x = 32$) and *V. miqueliana* Nakai (hexaploid, $2n = 6x = 48$) based on single reports for each. Two reports are available for *V. cana* Wall. with $2n = 50$ and $2n = 52$, which may be cases of increased chromosome number from $x = 8$, reductions from $x = 9$, or miscounts. Unfortunately, neither count is accompanied by a figure, which could have resolved the conflict. The chromosome number of the fourth species that has been investigated, $2n = 42$ for *V. robusta* (Prain) T. Yamaz., is also difficult to explain, but again may represent a miscount or an aberrant aneuploid individual, much less likely an independent reduction to $x = 7$. The scarcity and ambiguity of the data indicate the need to reinvestigate chromosome numbers coupled with DNA sequence data in order to infer the evolutionary trends in this group.

Veronica sect. *Veronica* can be divided in *Veronica* subsect. *Alpinae* Benth. (8 species), *V.* subsect. *Veronica* (5 species), and five other species across four other subsections. All these species have chromosome numbers based on $x = 9$ with the exception of *V. baumgartenii* Roem. & Schult. ($x = 7$; see below). Within *Veronica* subsect. *Alpinae*, *V. alpina* L., *V. nutans* Bong., *V. copelandii* Eastw., *V. stelleri* Pall. ex Link, and *V. nipponica* Makino are diploids ($2n = 2x = 18$; 37, nine, one, three, and one count, respectively, with one intrapopulational cytotype mixture: $2x$ and $4x$ in *V. alpina* in Norway; Knaben & Engelskjön, 1967), whereas *V. wormsjkoldii* Roem. & Schult. is exclusively tetraploid ($2n = 4x = 36$; four counts). *Veronica bellidioides* is mostly tetraploid ($2n = 4x = 36$; 36 counts including ours from the Pyrenees and Bulgaria), but diploid plants ($2n = 2x = 18$; seven counts) are known from the

western Pyrenees (Küpfer, 1968, 1974). Sampling is adequate in most species of subsection *Alpinae* except for *V. stelleri*, which has not been sampled in Alaska, U.S.A., and *V. nutans*, which has only been studied in California and Nevada, U.S.A., as well as in Canada but not in the northern Cascades or the phylogeographically important (Albach et al., 2006) southern Rocky Mountains. *Veronica cusickii* A. Gray is more problematic, with only two populations from the distributional extremes studied, one diploid ($2n = 2x = 18$) from California and one octoploid ($2n = 8x = 72$) from southwestern British Columbia.

Veronica officinalis L. has been studied intensively throughout Europe but not beyond the Siberian part of its range. Most chromosome numbers reported are tetraploid ($2n = 4x = 36$; more than 80 counts), with diploids ($2n = 2x = 18$) found in Portugal (Muñoz-Centeno et al., 2007), Gotland/Sweden (Böcher, 1944), and in the east Siberian Sayan Mountains (Stepanov, 1994), the only count outside Europe. Reports of $2n = 32$ or 34 (Gadella & Kliphuis, 1963, 1966; Kliphuis & Wieffering, 1972; Rossitto et al., 1983) likely represent miscounts (voucher specimens for the first three studies have been checked; Albach, unpublished data). However, this is difficult to prove since only Rossitto et al. (1983) presented a figure, which arguably shows 35 chromosomes. The other four species in subsection *Veronica* have a fairly restricted distribution. *Veronica allionii* Vill. from the southwestern Alps is diploid ($2n = 2x = 18$; three counts), whereas *V. onoei* Franch. & Sav. from Japan is tetraploid ($2n = 4x = 36$; two counts). *Veronica dabneyi* Hochst. from the Azores and *V. morrisonicola* Hayata from Taiwan have not been studied yet.

The five remaining species in subgenus *Veronica* are more problematic. *Veronica aphylla* L. has been reported as diploid ($2n = 2x = 18$; 11 counts) in the Alps, Pyrenees, and Tatra mountains. The closely related *V. grandiflora* Gaertn. from around the Bering Strait has been reported to have $2n = 48$ – 50 chromosomes, a number that cannot be associated with a regular ploidy level based on $x = 9$. *Veronica urticifolia* Jacq. is diploid ($2n = 2x = 18$; eight counts). Reports of $2n = 64$ (Meškova, 1965; Nilsson & Lassen, 1971) probably refer to misidentified *V. teucrium* L., although at least the voucher of one study (Nilsson & Lassen, 1971) was confirmed to be *V. urticifolia* (Fischer, unpublished data). A count of $2n = 16$ by Mattick (in Tischler, 1950) appears dubious and impossible to verify since no voucher specimen is indicated. Three studies have published chromosome numbers for *V. ponaë* Gouan from the Pyrenees and northern Spain. It was reported as hexaploid ($2n = 6x = 54$; Küpfer, 1972, 1974) in five populations (also confirmed by us, see Table 1) and diploid ($2n = 2x =$

16–18; Huber, 1927) in one. Unfortunately, no voucher specimen for the diploid count, which was grown in a botanical garden (Dilger-Endrulat, at TUB, pers. comm.), is known. It may be a misidentified *V. urticifolia*. Finally, *V. baumgartenii* (from the Carpathians) is inferred to have the deviating chromosome base number $x = 7$ ($2n = 2x = 14$; two counts), although it is mostly considered closely related to *V. aphylla*, a relationship not seen in DNA sequence analyses (Albach, unpublished data).

II. VERONICA SUBG. BECCABUNGA

This subgenus consists of three sections. The aquatic species of section *Beccabunga* (Hill) Dumort. are sister to sections *Acinifolia* (Römpf) Albach and *Serpyllifolia* G. Don (Albach et al., 2004a, 2005a; Fig. 2). Whereas species of the former section have a chromosome base number of $x = 9$, the plesiomorphic number for the subgenus (Albach et al., 2004a) and species of the other two sections have a base number of $x = 7$. Our results of $2n = 2x = 18$ and $2n - 2x = 36$ ($x = 9$) for *V. hispidula* Boiss. & Huet. are important in that respect because it has been considered to be a member of section *Acinifolia* (Römpf, 1928; Fischer, 1972). The different chromosome base number, however, agrees with its position in analyses of DNA sequences in which it is sister to the rest of the subgenus (Albach, unpublished data; see Fig. 2). It is therefore considered as having an uncertain position within the subgenus here.

Species boundaries in section *Beccabunga* have been interpreted differently by different authors (Borissova, 1955; Fischer, 1981); the species are treated here in a narrow sense with 13 species in the section. Vagueness of species boundaries is exemplified by—and based on—the apparent existence of different ploidy races in several species, which could either be due to cryptic taxa not recognized on basis of morphology or due to misidentification or misinterpretation of taxa. In subsection *Beccabunga*, *Veronica beccabunga* L. is diploid ($2n = 2x = 18$; subspecies *beccabunga* L., more than 50 counts; subspecies *abscondita* M. A. Fisch., three counts; subspecies *muscosa* (Korsh.) Elenevsky, one count), but tetraploid numbers ($2n = 4x = 36$) have been reported for subspecies *beccabunga* from Poland (Sokolowska in Skalinska, 1964), Italy (Ferrarella et al., 1981), and Sweden (Lökvist & Hultgard, 1999) and most likely represent autotetraploids. Counts of $2n = 2x = 16$ for subspecies *beccabunga* (Davlianidze, 1980) and subspecies *muscosa* (Sokolovskaja & Strelkova, 1939 according to Agapova et al., 1993) are probably miscounts. The close relative *V. americana* Schwein. ex Benth. is tetraploid ($2n = 4x = 36$; 12 counts).

Veronica anagallis-aquatica L. and its relatives are morphologically more difficult to differentiate, which is reflected in incorrectly determined specimens used for chromosome counts. *Veronica lysimachioides* Boiss. seems to be a diploid species ($2n = 2x = 18$; six counts), whereas *V. anagallis-aquatica*, *V. michauxii* Lam., and *V. catenata* Pennell are tetraploids ($2n = 4x = 36$; more than 70, five and 16 counts, respectively) and *V. undulata* Wall. is hexaploid ($2n = 6x = 54$; 12 counts). *Veronica oxycarpa* Boiss. seems to be another tetraploid species ($2n = 4x = 36$; six counts), but a diploid count ($2n = 2x = 18$) is reported by Meškova (1965; see Öztürk & Fischer [1982] for doubts regarding this count). The correct chromosome number for *V. poljensis* Murb. is unknown. Marchant (1970) states that it is diploid ($2n = 2x = 18$), but his figures show it to be tetraploid. Öztürk and Fischer (1982) report a tetraploid number, but state that their specimen is intermediate between *V. poljensis* and *V. anagalloides* Guss. Dzhus and Dmitrieva (2001) report a diploid from Belarus, but the species is not known from that area or near it and, therefore, may be a misidentified *V. anagalloides*. This species is diploid ($2n = 2x = 18$; subspecies *anagalloides* Guss., 10 counts; subspecies *heureka* M. A. Fisch., 10 counts including the report here). However, several tetraploid counts have been published. Meškova's (1965) tetraploid count ($2n = 4x = 36$) from Ukraine has been considered improbable by Öztürk and Fischer (1982), and no voucher could be located. The voucher specimen for the tetraploid count from Afghanistan (Podlech & Dieterle, 1969) does not resemble the typical subspecies *heureka* (Öztürk & Fischer, 1982), but the one from Yemen (Podlech, 1986) does (Albach, pers. obs.). The voucher specimens from Romania (Vasudevan, 1975), Pakistan (Khatoon, 1991, in Khatoon & Ali, 1993), and Iran (Saeidi-Mehrvarz & Kharabian, 2005) have not been checked. Information on the voucher is only given for the number from Iran. Based on this information, it is probable that tetraploid taxa of *V. anagalloides* subsp. *heureka* ($2n = 4x = 36$) exist in southwest Asia. Sánchez-Agudo, Delgado, and Martínez-Ortega (in prep.) recently found tetraploid chromosome numbers ($2n = 4x = 36$) from Spain. Their status needs further attention. The same is true for tetraploid counts of *V. anagalloides* subsp. *heureka* from Russian Far East ($2n = 4x = 36$; Probatova et al., 1996), which is by far the easternmost occurrence of this taxon. Differentiation of this taxon is often difficult as plants often resemble diminutive *V. anagallis-aquatica*. *Veronica scardica* Griseb. is another species for which two ploidy levels are reported. Marchant (1970) reports diploid chromosome numbers ($2n = 2x = 18$) from several countries

without further documentation. This ploidy level was also reported by Öztürk and Fischer (1982) from Turkey. Strid and Franzén (in Löve, 1981) and van Loon and van Setten (in Löve, 1982), however, report tetraploid plants ($2n = 4x = 36$) from the Balkan Peninsula. The identity of the voucher specimen for the first tetraploid plant has been confirmed; the one for the second shows a mixture of characters and is not clearly identifiable but is definitely not pure *V. scardica*. *Veronica scardica* is a serpentinophyte that might be only an ecological race of *V. anagalloides* or *V. anagallis-aquatica* (Fischer et al., 1984), which could explain the different ploidy levels reported. Detailed morphological and karyological analyses together with cultivation experiments will be necessary to solve the systematic questions regarding this species.

Finally, the annual *Veronica peregrina* L., the only member of subsection *Peregrinae* Elenevsky, was also shown to be a member of section *Beccabunga* (Albach & Chase, 2001; Albach et al., 2004a). Eleven counts confirm its chromosome number of $2n = 6x = 52$, which was hypothesized to be derived from $2n = 6x = 54$ by chromosome fusion (cf. Hofelich, 1935; Albach et al., 2004a). The count of $2n = 54$ by Chuang and Heckard (1992) from Oregon is interesting in that respect because it may represent a lineage that diverged before the fusion of the chromosomes occurred. Alternatively, it may be a miscount, but no figure is included in the publication.

Section *Acinifolia* comprises eight species (without *Veronica hispidula*, which we exclude). Previously, chromosome numbers were known for four species, the diploid ($2n = 2x = 14$) *V. acinifolia* L., *V. pusilla* Kotschy & Boiss., and *V. syriaca* Roem. & Schult. (11, three and three counts, respectively) and the tetraploid *V. bozakmanii* M. A. Fisch. ($2n = 4x = 28$; six counts including the report here). We add here information on a fifth species, *V. reuteriana* Boiss., for which within one population two plants showed the tetraploid level ($2n = 4x = 28$) and one plant the hexaploid level ($2n = 6x = 42$). Intraspecific ploidy level variation in *V. hispidula* and *V. reuteriana* is noteworthy. No morphological character corresponding to different ploidy levels has been noted but should be looked for in future investigations. Chromosome numbers in other rare species from southwest Asia are still unknown.

Sister to section *Acinifolia* is section *Serpyllifolia* in subgenus *Beccabunga*, a group including only perennial taxa, which probably shares the ancestral chromosome base number of $x = 7$ (Fig. 2). This subsection includes 11 species. Chromosome numbers are available for five taxa. These include the diploid *V. telephiifolia* Vahl ($2n = 2x = 14$; one count), *V.*

serpyllifolia L. (more than 70 counts; including subspecies *repens* (Clarion ex DC.) Hartl in Hegi from Corsica), and *V. nevadensis* var. *langei* (Lacaita) M. M. Mart. Ort. & E. Rico (six counts), which form subsection *Serpyllifolia* (G. Don) Stroh. Mattick (in Tischler, 1950) and Peev (1975) report tetraploid counts ($2n = 4x = 28$) for *V. serpyllifolia* from Austria and Bulgaria, respectively, which may be spontaneous autotetraploids, but a voucher specimen for the first report is not indicated and those from Peev have not been checked. A count of $2n = 2x = 16$ by Probatova and Sokolovskaya (1990) is probably a miscount. Unfortunately, no figure is presented.

The polyploid complex of *Veronica gentianoides* Vahl, classified as subsection *Gentianoides* (G. Don) Assejeva, is without a doubt the most complex group karyologically in the genus. Eight different ploidy levels on two different base numbers have been published, and our report of $2n = 36$ presents the ninth ploidy level (with a range of $2x$ – $10x$). Tumadjanov has studied this group extensively (e.g., Tumadjanov & Beridze, 1969; Tumadjanov et al., 1977), but questions still remain, partly due to the limited documentation of chromosome counts in his studies. Tumadjanov et al. (1977) proposed an intraspecific base number switch from $x = 8$ to $x = 12$, with $x = 8$ predominating in the Turkish and Armenian distribution area and $x = 12$ in the Greater Caucasus and Georgian Lesser Caucasus. However, this distinction is refuted by his own data. The ancestral diploid race ($2n = 2x = 16$) is found in the northern Colchis, a suggested refugium for tertiary forest species (Tumadjanov & Beridze, 1969). Other chromosome numbers based on $x = 8$ found in the Greater Caucasus are: $2n = 4x = 32$ (throughout the species range; Tumadjanov & Beridze, 1969; Tumadjanov et al., 1972), $2n = 5x = 40$ (Tumadjanov et al., 1972), $2n = 7x = 56$ (Western Caucasus; Magulaev, 1984), $2n = 8x = 64$ (Azerbaijan; Tumadjanov & Beridze, 1969 from Central Caucasus; Kliphuis in Löve, 1979), and $2n = 10x = 80$ (Georgian parts of the Lesser Caucasus; Tumadjanov & Beridze, 1969; Tumadjanov et al., 1972). Other chromosome numbers of the Greater Caucasus are more compatible with a base number of $x = 12$. The related *V. schistosa* E. Busch ($2n = 24$; six counts) is either a diploid ($x = 12$) or a triploid ($x = 8$). Zakharjeva (in Agapova et al., 1993) counted $2n = 48$ (tetraploid or hexaploid, respectively) for this species, but no voucher specimen is indicated. Therefore, we cannot be sure about its identity, and it may be a count for the closely related *V. gentianoides* in which this number is common. According to Tumadjanov et al. (1972, 1977), the predominating polyploid races in *V. gentianoides* in the Greater Caucasus have $2n = 24$ (either $2x$ or $3x$),

$2n = 48$ (either $4x$ or $6x$), and $2n = 72$ ($6x$ or $9x$), the latter two confirmed by us. Our report of $2n = 36$ is, however, the first that is incompatible with a hypothesis of a basic chromosome number of $x = 8$ in *V. gentianoides* in the Greater Caucasus and suggests instead $x = 12$. The predominating polyploid races in the Lesser Caucasus (especially Armenia) have $2n = 32$ and 48 , although data from Turkey are lacking. Various species have been segregated from *V. gentianoides* by some authors (e.g., Kemularia-Nathadze, 1955), but no information on ploidy level for these segregates is available.

III. VERONICA SUBG. PSEUDOLYSIMACHIUM

This subgenus includes 26 species, with chromosome numbers known for 18. In contrast to the case in *Veronicastrum* and *Picrorhiza*, the derived chromosome base number $x = 17$ likely originates from the combination of two genomes with $2n = 18$ with a subsequent reduction to $2n = 17$ based on its phylogenetic position distant to any taxon with $x = 8$ (Fig. 2) and karyological observations by Graze (1935). The origin of the base chromosome number $x = 17$ has been further discussed by Albach et al. (2004a). To highlight the fact that it is a derived base chromosome number for *Veronica* subg. *Pseudolysimachium* alone, it will subsequently be denoted as x_{psl} ($= 2x$). Seven of the species in the subgenus are diploid ($2n = 2x_{psl} = 34$), two are tetraploid ($2n = 4x_{psl} = 68$), and seven include both diploid and tetraploid populations. The tetraploid level for *V. spuria* L. (Peev in Löve, 1972b) needs confirmation because unfortunately voucher information given in the publication and specimens in the herbarium do not match (M. A. Fischer, pers. obs.). Chromosome numbers of the European species have recently been reviewed by Travníček et al. (2004) and Albach and Fischer (2003). In Asia, only diploids ($2n = 2x_{psl} = 34$) of *V. daurica* Steven, *V. linariifolia* Pall. ex Link., *V. kiusiana* subsp. *miyabei* (Nakai & Hondo) T. Yamaz., *V. nakaiana* Ohwi, *V. pinnata* L., and *V. schmidtiana* Regel and tetraploids ($2n = 4x_{psl} = 68$) of *V. kiusiana* subsp. *maritima* (Nakai) T. Yamaz., *V. ornata* Monjuschko, and *V. subsessilis* (Miq.) Carriere are known mostly from single counts. Chromosomes of the species in this subgenus are extremely small and sticky, which makes the correct determination of chromosome numbers difficult (cf. Weiss et al., 2002). Deviations from $2n = 2x_{psl} = 34$ or $2n = 4x_{psl} = 68$ by one or two chromosomes are consequently more common than in other subgenera. Unfortunately, the first publication of chromosome numbers in *Veronica* (Heitz, 1926) already includes a dubious count, $2n = 48$ for *V. azurea* Link (a synonym of *V. longifolia* L.).

The figure shows 48 to 50 chromosomes, but clearly not the expected 34 or 68 chromosomes. No voucher information is included, so this count remains doubtful. Other doubtful records that require further investigation are those for *V. grandis* Fisch. ($2n = 56$; Zhukova, 1967, according to Agapova et al., 1993), *V. olgensis* Kom. ($2n = 24$; Gurzenkov, 1973, likely to be a printing error for $2n = 34$), and *V. sajanensis* Printz ($2n = 18$; Malachova, 1971; Krasnoborov, 1976; both according to Krogulevich and Rostovtseva, 1984) and those by Androschuk (1988). The counts by Androschuk (1988) appear to have a systematic error because nine different species have been investigated and all counts are based on $x = 9$ and not on $x = 17$ as expected for subgenus *Pseudolysimachium*. A count of $2n = \text{ca. } 90$ for *V. longifolia* from Yakutia by Krogulevich and Rostovtseva (1984) also appears dubious. Future research on the European species of this subgenus needs to focus on the origin of tetraploids, whereas more fundamental information on chromosome numbers and morphology is necessary for the Asian species of the subgenus.

IV. VERONICA SUBG. SYNTHYRIS

Chromosome numbers are known for all species of *Veronica* subg. *Synthyris*. They all share the chromosome base number of $x = 12$, which is rare in Veroniceae with all extant relatives suggested by phylogenetic analyses (e.g., Albach et al., 2004a; Fig. 2) having $x = 9$. Lepper (1964), based on karyotype analysis, suggested that the number represents a diploid level with aneuploid chromosome number increase. However, the alternative that the number is derived from an ancestor with $2n = 2x = 14$ followed by reduction to $n = 6$ in gametes and perhaps production of unreduced gametes and subsequent polyploidization should not be discarded because of the frequent parallel reductions to $x = 7$ in *Veronica* (see above). Most species are diploid ($2n = 2x = 24$), but *V. ritteriana* (Eastw.) M. M. Mart. Ort. & Albach and *V. canbyi* (Pennell) M. M. Mart. Ort. & Albach are tetraploid ($2n = 4x = 48$), and, in *V. missurica* subsp. *major* (Hook.) M. M. Mart. Ort. & Albach, *V. missurica* subsp. *stellata* (Pennell) M. M. Mart. Ort. & Albach, *V. plantaginea* E. James, and *V. wyomingensis* (A. Nelson) M. M. Mart. Ort. & Albach, both diploid and tetraploid plants have been found in different populations.

V. VERONICA SUBG. COCHLIDIOSPERMA

Veronica subg. *Cochlidiosperma* is the group with the most counts per species. With the exception of *V. sibthorpioides* Deb., Degen & Hervier, all species

share the chromosome base number $x = 9$. *Veronica sibthorpioides*, a species from southern Spain and Morocco, however, has $2n = 30$ as confirmed by 14 counts from different localities, although Sánchez-Agudo et al. (unpublished data) recently reported two counts of $2n = 28$. Several species are diploid ($2n = 2x = 18$): *V. crista-galli* Steven (three counts), *V. stewartii* Pennell (two counts), *V. triloba* Opiz (25 counts), *V. stamatiadae* M. A. Fisch. & Greuter (one count), *V. lycica* E. B. J. Lehm. (one count), *V. panormitana* Tineo (six counts), and *V. trichadena* Jord. & Fourr. (seven counts). A count (Peev in Löve, 1972a) from Bulgaria of *V. hederoides* M. A. Fisch. (a synonym of *V. stewartii* from the Himalayas; $2n = 2x = 18$) refers to *V. triloba* (Fischer, 1984). Counts of $2n = 2x = 18$ for *V. sublobata* M. A. Fisch. and *V. hederifolia* L. by Nordenstam and Nilsson (1969) and Guo and Liu (2001), respectively, probably also refer to *V. triloba*, but the vouchers have not been checked. The proposed separation of *V. sublobata* from *V. hederifolia* s. str. (Fischer, 1967), partly based on its lower ploidy level (tetraploid vs. hexaploid), has led to numerous new reports (more than 100 populations counted for each taxon) for these two species, especially in The Netherlands (de Jongh & Kern, 1973; Gadella & Kliphuis, 1976) and northern Europe (Nordenstam & Nilsson, 1969; Fischer, 1975b), showing a rather perfect correlation between tetraploidy in *V. sublobata* and hexaploidy in *V. hederifolia* s. str. and a clear-cut separation between these species. The few early deviating counts in northern Europe (Nordenstam & Nilsson, 1969) were due to insufficiently careful identification of the investigated specimens. Morphological differentiation between *V. sublobata* and *V. hederifolia* s. str. seems to be more difficult, however, in some southern regions of Europe where chromosome counts are still scarce (Sánchez-Agudo et al., unpublished data). *Veronica sublobata* is a tetraploid ($2n = 4x = 36$) derivative of *V. triloba* (Fischer, 1975b; Albach, unpublished data). Hybridization between *V. triloba* and *V. sublobata* gave rise to the hexaploid ($2n = 6x = 54$) *V. hederifolia* (Albach, unpublished data). A count of $2n = 56$ by Meškova (1965) is probably a miscount, but unfortunately, this publication was inaccessible to us. Counts of $2n = 26$ to 28 (Sorsa, 1963; Gadella & Kliphuis, 1966) probably refer to *V. persica*, which often grows side by side with *V. hederifolia*. No voucher is indicated by Sorsa (1963) and the voucher from Gadella and Kliphuis (1966) has not been checked. A tetraploid count ($2n = 4x = 36$) for *V. hederifolia* from Iran (Saeidi-Mehrvarz & Kharabian, 2005) is of interest because *V. sublobata* is not known from that region. This may represent a different taxon and requires further confirmation. A publication from Guo and Liu

(2001) provided a range of chromosome numbers for *V. hederifolia* from its introduced range in Nanjing, China, including diploids ($2n = 2x = 18$), tetraploids ($2n = 4x = 36$), and hexaploids ($2n = 6x = 54$), as well as more unexpected numbers: $2n = 22, 32$. Their drawings in the paper indicate the reported chromosome numbers. It is not clear how an aneuploid chromosome race could have arisen in the short time since its introduction, and a mix-up of the samples with another weedy species with $2n = 32$ during the collection or processing is considered most likely.

Veronica cymbalaria Bodard is karyologically more difficult. Tetraploid ($2n = 4x = 36$) and hexaploid ($2n = 6x = 54$) plants are morphologically indistinguishable (Fischer, 1975a), and both ploidy levels originated more than once from *V. panormitana* and two different clades of *V. trichadena* (Albach, 2007). A map of the origins of 38 known tetraploid and 24 known hexaploid plants of *V. cymbalaria* will be published elsewhere. Counts of $2n = 2x = 18$ by Hofelich (1935) and Nilsson and Lassen (1971) probably refer to *V. trichadena* or *V. panormitana*, but a voucher for the first could not be found (Dilger-Endrulat, at TUB, pers. comm.; Albach, pers. obs.) and the other has not been checked.

VI. VERONICA SUBG. PELLIDOSPERMA

This subgenus is a small group of seven annual species. Chromosome numbers for *Veronica donii* Römpf, *V. aznavourii* Dörfl., and *V. samuelssonii* Rech. f. are not available but would be highly desirable because, amazingly, three different base numbers ($x = 7, 8, 9$) have been reported so far in this subgenus with all taxa reported as diploid. *Veronica triphyllos* L. has $2n = 2x = 14$ (18 counts); *V. praecox* All. and *V. glauca* Sibth. & Sm. have $2n = 2x = 18$ (19 and five counts, respectively); and *V. mazanderanae* Wendelbo, a species endemic to Iran, has $2n = 2x = 16$ (one count).

VII. VERONICA SUBG. STENOCARPON

This subgenus includes 31 montane to alpine species of Eurasia and Mexico. Chromosome numbers are known for all eight European species but only for two Asian species (*V. ciliata* Fisch., *V. densiflora*). All chromosome numbers are based on $x = 8$ and represent diploids ($2n = 2x = 16$) with the exception of the tetraploid ($2n = 4x = 32$) *V. contandriopouli* Quézel from Greece, which is possibly just an aberrant specimen of autotetraploid *V. erinoides* Boiss. & Spruner. *Veronica fruticans* Jacq. is the best studied species (31 counts throughout its distribution area in the European high mountain ranges). For all other

species, less than five counts per species have been published (*V. ciliata*, four counts including the report here; *V. densiflora*, four counts; *V. erinoides*, one count; *V. fruticulosa* L., three counts; *V. mampodrensis* Losa & P. Monts., one count; *V. nummularia* Gouan, three counts including the report here; *V. saturejoides* Vis., three counts; *V. thessalica* Benth., two counts). Our count of $2n = 2x = 16$ for *V. ciliata* from the southeasternmost distribution range confirms those from other extremes of the distribution.

VIII. VERONICA SUBG. POCILLA

Veronica subg. *Pocilla* (Dumort.) M. M. Mart. Ort., Albach & M. A. Fisch. includes 27 annual and one perennial species including the well-known cosmopolitan weed *V. persica*. The chromosome base number for the 15 species counted is $x = 7$, although it is not clear for *V. cardiocarpa* (Kar. & Kir.) Walp., for which the only publication states $2n = 14$ –16 (Hofelich, 1935), and *V. campylopoda* Boiss. (see below). Chromosome numbers are known for over half of the species, especially the weedy species (*V. persica*, 48 counts; *V. polita* Fr., 38 counts; *V. agrestis* L., 22 counts; *V. filiformis* Sm., 12 counts; and *V. opaca* Fr., 11 counts). Diploids ($2n = 2x = 14$) include *V. polita* (sometimes under its synonym *V. didyma* Ten.), *V. cardiocarpa* (one count), *V. ceratocarpa* C. A. Mey. (three counts), *V. filiformis*, *V. francispetae* M. A. Fisch. (two counts), and *V. siaretensis* E. B. J. Lehm. (one count). *Veronica persica*, *V. agrestis*, *V. opaca*, *V. biloba* L. (three counts), *V. capillipes* Nevski (two counts), and *V. rubrifolia* Boiss. (two counts) are tetraploids ($2n = 4x = 28$). Taxonomic history, especially in Asia, confused *V. agrestis* with *V. polita* for a long time (Lehmann, 1910, 1940), and, consequently, several publications from the same authors in India state a diploid level for *V. agrestis* (e.g., Bir & Sidhu in Löve, 1978). Probably all of these publications refer to *V. polita*, which is common in Asia, rather than *V. agrestis*, which occurs exclusively in Europe. A report of $2n = 2x = 18$ for *V. polita* from Hungary (Borhidi, 1968) is probably due to confusion with *V. triloba*, but no voucher specimen is indicated.

Regarding *Veronica* sect. *Subracemosae* (Benth.) Assejeva in subgenus *Pocilla*, our count of $2n = 6x = 42$ is the third report confirming the hexaploid level for *V. arguteserrata* Regel & Schmalh. *Veronica campylopoda* is the only species in this subgenus and one of four in the genus for which more than two ploidy levels have been reported in the literature. Fischer (1981) reported a tetraploid ($2n = 4x = 28$) plant from Iran. Nine counts of hexaploid plants ($2n = 6x = 42$) originate from Central Asia to the Mediterranean, with our count being the first from Turkey. Our report of an

octoploid plant ($2n = 8x = 56$) is the second for that ploidy level in *V. campylopoda*, with both notably from Turkey. Reports of $2n = 2x = 18$ from Afghanistan (Podlech & Dieterle, 1969) and $2n = 4x = \text{ca. } 36$ from Utah, U.S.A. (Bell, 1965), where it is introduced, appear dubious in light of other reports, but voucher specimens for the first count have been confirmed by the first author. The voucher specimen for the second belongs to *V. arguteserrata*. However, such morphological intergradation is typical for well-watered specimens of *V. campylopoda* (Albach, unpublished data).

IX. VERONICA SUBG. PENTASEPALAE

Subgenus *Pentasepalae* (Benth.) M. M. Mart. Ort., Albach & M. A. Fisch. is by far the largest subgenus of *Veronica* in the Northern Hemisphere, with 72 species most common in southwest Asia. Chromosome numbers are available for 32 taxa including all European species. All species investigated have a base chromosome number of $x = 8$, including 19 diploids ($2n = 2x = 16$), five tetraploids ($2n = 4x = 32$), one hexaploid ($2n = 6x = 48$), and three octoploids ($2n = 8x = 64$). European and Siberian species are classified within *Veronica* subsect. *Pentasepalae* Benth. and represent several, often ancestral, diploid species (*V. crinita* Kit. ex Schult., two counts; *V. kindlii* Adamović, one count; *V. krylovii* Schischk., one count; *V. orbelica* (D. Peev) D. Peev, one count; *V. orsiniana* Ten., 14 counts; *V. prostrata* L., 20 counts including the reports here; *V. rhodopea* (Velen.) Degen ex Stoj. & Stef., one count; *V. rosea* Desf., 13 counts; *V. tenuifolia* Asso, 16 counts; *V. turrilliana* Stoj. & Stef., three counts). Polyploid species include *V. aragonensis* Stroh, *V. scheereri* (J. P. Brandt) Holub ($2n = 4x = 32$; six and 24 counts, respectively), and *V. sennenii* (Pau) M. M. Mart. Ort. & E. Rico ($2n = 8x = 64$; six counts). For the three most widespread species of *Veronica* subsect. *Pentasepalae*, several ploidy levels have been reported. *Veronica teucrium* is octoploid ($2n = 8x = 64$) with one publication reporting diploid plants ($2n = 2x = 16$) from southern France (Küpfer, 1969), possibly belonging to *V. orsiniana*, and one hexaploid plant ($2n = 6x = 48$) from Germany (Lippert & Heubl, 1989). Voucher specimens for the hexaploid plants have been checked and represent *V. teucrium* rather than the sympatric *V. austriaca* L., which is mostly hexaploid except for some specimens from southwestern Germany and northwestern Switzerland (Brandt, 1952, 1961). However, intermediates between *V. teucrium* and *V. austriaca* are known from southwestern Germany; therefore, these populations need further study in a wider context. The third species of the subsection, which is widespread and karyologically polymorphic, is *V. jacquinii* Baumg., for which octoploid plants ($2n = 8x = 64$) are reported

from Greece (Strid in Löve, 1986b). Other reports for this species are mostly hexaploid ($2n = 6x = 48$; 13 counts), with a diploid race ($2n = 2x = 16$) reported from Albania (Baltisberger, 1988) and tetraploid ($2n = 4x = 32$) and decaploid races ($2n = 10x = 80$) reported from Bulgaria (Peev, 1972). Pinnatifid leaves have evolved multiple times independently in *Veronica* (Albach et al., 2004c) and may even have evolved independently in taxa of different ploidy levels, but all are considered here under *V. jacquinii*.

The same is true for *Veronica multifida* L. of *Veronica* subsect. *Orientalis* (Wulff) Stroh, a taxon with species mainly found in Turkey. Diploid plants ($2n = 2x = 16$) of *V. multifida* have been reported from Bulgaria (Peev in Löve, 1972b) and southern Turkey (Fischer, 1970), tetraploids ($2n = 4x = 32$) from Armenia (Meškova, 1965) and southern Turkey (Fischer, 1970), hexaploids ($2n = 6x = 48$) from southwestern Turkey (Fischer, 1970), and decaploids ($2n = 10x = 80$) from Armenia (Gukasian & Safarian, 1990). *Veronica multifida* is a highly polymorphic species, but no morphological correlate to the different ploidy races has been found (Fischer, 1970). In this respect, *V. multifida* resembles *V. orientalis* Mill., another morphologically polymorphic species from southwest Asia with several ploidy levels reported. A tetraploid plant ($2n = 4x = 32$) has been reported from Armenia (Meškova, 1965) and octoploids ($2n = 8x = 64$) from Iran (Ghaffari in Löve, 1986a) and Israel (Pazy, 2000). The closely related *V. kurdica* Benth. is hexaploid ($2n = 6x = 48$; one count). Other species of the subsection are mostly diploid ($2n = 2x = 16$; *V. bombycina* Boiss. & Kotschy, two counts including the report here; *V. caespitosa* Boiss., two counts; *V. cinerea* Boiss. & Balansa, two counts; *V. cuneifolia* D. Don, one count; *V. dichrus* Schott & Kotschy, three counts; *V. farinosa* Hausskn., one count; *V. macrostachya* Vahl subsp. *sorgerae* M. A. Fisch., one count; *V. pectinata* L., one count) with only *V. elmaliensis* M. A. Fisch. being octoploid ($2n = 8x = 64$, one count).

Chromosome numbers for the ca. 30 species of the five remaining subsections of *Veronica* subg. *Pentasepalae* are lacking except for two, the diploid taxon *V. peduncularis* M. Bieb. ($2n = 2x = 16$, three counts) and the tetraploid *V. microcarpa* Boiss. ($2n = 4x = 32$, one count). Future research should especially focus on southwest Asia and the Caucasus since those taxa for which no chromosome number is yet available occur in Turkey (18 species), Iran (12 species), and the Greater Caucasus (10 species).

X. VERONICA SUBG. CHAMAEDRYIS

Veronica subg. *Chamaedryis* is one of the best studied groups in *Veronica* including one of the best studied species (*V. chamaedryis* L., with more than 90

counts). All species have chromosome numbers based on $x = 8$ except for *V. magna*, which appears to have $x = 7$ (see below). Only *V. sartoriana* Boiss. & Heldr., a Greek endemic closely related to *V. arvensis* L., has not been studied. The annual members of this subgenus, *V. arvensis* (42 counts), *V. verna* L. (17 counts), *V. dillenii* Grantz (12 counts), and *V. brevistyla* Moris (two counts), are all diploid ($2n = 2x = 16$). A count of $2n = 14$ for *V. arvensis* was reported by Löve and Löve (1956) from Iceland. Unfortunately, neither a figure of the chromosomes is given nor a voucher specimen indicated. Therefore, we cannot check our assumption of a miscount or a mix-up with *V. polita*. The European perennial species are also diploid with the exception of *V. chamaedrys* subsp. *chamaedrys*, which is tetraploid ($2n = 4x = 32$). However, within *V. chamaedrys* subsp. *chamaedrys*, some diploid taxa are insufficiently known (Fischer, 1973; see Dobeš & Vitek, 2000 for a map) and several diploid plants cannot be clearly assigned to the described taxa (Bardy & Albach, unpublished data). Finally, the Caucasian *V. magna* seems to be hexaploid ($2n = 6x = 42$) and the Asian *V. laxa* Benth. has been reported to be either tetraploid ($2n = 4x = 32$; China) or hexaploid ($2n = 6x (-2) = 46$; Japan, India). More information on the latter would be desirable to investigate whether tetraploids and hexaploids can be differentiated and whether diploid progenitor taxa still exist within the species.

XI. VERONICA SUBG. PSEUDOVERONICA (HEBE COMPLEX)

Veronica subg. *Pseudoveronica* J. B. Armstr., established by Armstrong (1881), is the nomenclaturally correct name for the Australasian species of *Veronica* formerly grouped in *Hebe* Comm. ex Juss. and related genera (Garnock-Jones et al., 2007). Chromosome numbers for species of *Parahebe* W. R. B. Oliv. on New Zealand (Garnock-Jones & Lloyd, 2004), *Hebe* (Bayly & Kellow, 2006), and the Australian species (Briggs & Ehrendorfer, 2006) have recently been reviewed. Therefore, we will only comment on the numbers of New Guinean species and the more general picture. The Australasian species constitute a monophyletic group nested within the $x = 8$ clade (Fig. 2) and apparently derived from a single polyploidization event. Thus, the derived chromosome base number in the subgenus is denoted as x_{Hebe} ($= 6x$, see below). *Veronica* ($=$ *Detzneria*) *tubata* (Diels) Albach from New Guinea, which is sister to the remaining Australasian species in a cladistic analysis of morphological characters (Hong, 1984) and in some of the DNA-based phylogenetic analyses by Albach et al. (2005a), has $2n = 48$ (Borgmann,

1964). This would fit in with a hexaploid origin of the Australasian species or $2n = 38\text{--}42$ (Briggs & Ehrendorfer, 2006), which is more in line with reports for other species in the subgenus with chromosome numbers derived from $x_{\text{Hebe}} = 20$ and $x_{\text{Hebe}} = 21$. Wagstaff and Garnock-Jones (1998) have shown that $x_{\text{Hebe}} = 21$ is ancestral to $x_{\text{Hebe}} = 20$, which evolved twice, once in the main clade of *Hebe* on New Zealand and once in Australia. Further phylogenetic analyses (Wagstaff et al., 2002; Albach et al., 2005a) have demonstrated that two further changes to $x_{\text{Hebe}} = 20$ need to be assumed for *V. decora* (Ashwin) Garn.-Jones in New Zealand and *V. ionantha* Albach in New Guinea. A hexaploid origin of the subgenus would therefore require an inferred loss of six to 12 chromosomes in the various species of the subgenus. Our understanding of phylogenetic relationships of Veroniceae in Australia, which shows much greater karyological diversity than the species in New Zealand, is unfortunately too limited to allow further inferences. The phylogenetic relationships of those taxa for which DNA sequences are available, inferred by Wagstaff et al. (2002), and their chromosome numbers are shown in Figure 2. The 12 species of *Parahebe* in New Guinea likely originate from a single immigration of a species from New Zealand (Albach et al., 2005a), chromosome numbers are available from a single publication (Borgmann, 1964) for two species (*V. ionantha* ($=$ *P. ciliata* (Pennell) P. Royen & Ehrend.); $2n = 2x_{\text{Hebe}} = 40$; *V. albiflora*: $2n = 2x_{\text{Hebe}} = 42$).

XII. VERONICA SUBG. TRIANGULICAPSULA

This taxon includes two morphologically enigmatic annuals. They are difficult to place using molecular data (Albach et al., 2004a). Even karyologically, no relationship is discernible because both species, the diploid *Veronica grisebachii* Walters from Turkey and the tetraploid *V. chamaepithyoides* Lam. from Spain, have the unusual chromosome base number of $x = 6$.

THE REMAINING SPECIES IN VERONICA

Chromosome numbers are known for one species that has not been assigned to any subgenus. *Veronica javanica* Blume is $2n = 16$, similar to subgenus *Chamaedrys* with which it shares some morphological characters, especially seed ultrastructure (Muñoz-Centeno et al., 2006). However, neither nuclear ribosomal nor plastid DNA sequences show a relationship with the $x = 8$ clade (Albach et al., 2005a; Fig. 2), which suggests that it has gained this base number independently.

Chromosome numbers of the other species in *Veronica* that to date have not been placed confidently in any subgenus (*V. himalensis* D. Don, *V. monticola* Trautv., *V. ruprechtii* Lipsky, *V. simensis* Fresen., *V. tibetica* D. Y. Hong, and *V. viscosa* Boiss.) would be highly desirable.

NOMENCLATURAL CHANGES FOR *VERONICA*

For the purpose of providing a taxonomically ordered overview of chromosome numbers in Veroniceae, we provide a list (Appendix 1) resolved down to the subsectional level in *Veronica* including all species currently accepted by us. Three new names at the supraspecific level are used here for the first time, and the correct nomenclatural publication of these names is given here. The description of a new subsection for *V. anagallis-aquatica* and relatives will be published in the future.

Veronica sect. **Acinifolia** (Römpf) Albach, stat. nov.
Acinifolia Römpf in Repert. Spec. Nov. Regni Veg. Beih. 50: 60. 1928 [*Veronica Verwandtschaftsgruppe*]. TYPE: *Veronica acinifolia* L., Sp. Pl., ed. 2, 1: 19. 1762.

The clade is equivalent at rank to *Veronica* sect. *Beccabunga* and *Veronica* sect. *Serpyllifolia* but has not been used at the sectional level yet.

Veronica sect. **Glandulosae** (Römpf) Albach, stat. nov.
Glandulosae Römpf, in Repert. Spec. Nov. Regni Veg. Beih. 50: 33. 1928 [*Veronica Verwandtschaftsgruppe*]. TYPE: *Veronica glandulosa* Hochst. ex Benth., Prodr. (DC.) 10: 482. 1846.

The same rationale as above applies in this case.

Veronica subsect. **Cochlidiosperma** (Rchb.) Albach, stat. nov.
Cochlidiosperma Rchb., Fl. Germ. Excurs.: 365. 1831–1832 [*Veronica* (unranked infragenus)]. TYPE (designated by Pouzar, 1964): *Veronica hederifolia* L., Sp. Pl. 1: 13. 1753.

Veronica hederifolia has traditionally been placed in subsections, whose type now belongs in subgenus *Pocilla*. To distinguish the blue-flowering species of *Veronica* sect. *Cochlidiosperma* from the white-flowering species (*Veronica* subsect. *Cymbalariae*), a new subsection needs to be established.

Literature Cited

Agapova, N. D., K. B. Arkharova, L. I. Vakhtina, E. A. Zemskova & L. V. Tarvis. 1993. Numeri chromosomatum Magnoliophytorum Florae URSS: Moraceae–Zygophyllaceae. Russian Academy of Science, St. Petersburg.

- Albach, D. C. 2007. The use of AFLP and sequence data in the phylogenetic analysis of polyploids: Multiple origins of *Veronica cymbalaria* (Plantaginaceae). *New Phytol.* 176: 481–498.
- & M. W. Chase. 2001. Paraphyly of *Veronica* (Veroniceae; Scrophulariaceae): Evidence from the internal transcribed spacer (ITS) sequences of nuclear ribosomal DNA. *J. Pl. Res.* 114: 9–18.
- & M. A. Fischer. 2003. AFLP- and genome size analyses: Contribution to the taxonomy of *Veronica* subg. *Pseudolysimachium* sect. *Pseudolysimachion* (Plantaginaceae), with a key to the European taxa. *Phytol. Balcan.* 9: 401–424.
- & M. W. Chase. 2004. Incongruence in Veroniceae (Plantaginaceae): Evidence from two plastid and a nuclear ribosomal DNA region. *Molec. Phylogen. Evol.* 32: 183–197.
- & J. Greilhuber. 2004. Genome size variation and evolution in *Veronica*. *Ann. Bot.* 94: 897–911.
- , M. M. Martínez-Ortega, M. A. Fischer & M. W. Chase. 2004a. Evolution of Veroniceae: A phylogenetic perspective. *Ann. Missouri Bot. Gard.* 91: 275–302.
- , ———, ——— & ———. 2004b. A new classification of the tribe Veroniceae—Problems and a possible solution. *Taxon* 53: 429–452.
- , ——— & M. W. Chase. 2004c. *Veronica*: Parallel morphological evolution and phylogeography in the Mediterranean. *Pl. Syst. Evol.* 246: 177–194.
- , T. Utteridge & S. J. Wagstaff. 2005a. Origin of Veroniceae (Plantaginaceae, formerly Scrophulariaceae) on New Guinea. *Syst. Bot.* 30: 412–423.
- , S. R. Jensen, F. Özgökçe & R. J. Grayer. 2005b. *Veronica*: Chemical characters for the support of phylogenetic relationships based on nuclear ribosomal and plastid DNA sequence data. *Biochem. Syst. Ecol.* 33: 1087–1106.
- , P. Schönswetter & A. Tribsch. 2006. Comparative phylogeography of the *Veronica alpina*-complex in Europe and North America. *Molec. Ecol.* 15: 3269–3286.
- Androschuk, A. F. 1988. Chromosome numbers in some species of the genus *Veronica* (Scrophulariaceae) in the Ukraine. *Bot. Zhurn.* 73: 454–455.
- Angiosperm Phylogeny Group. 2003. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG II. *Bot. J. Linn. Soc.* 141: 399–436.
- Armstrong, J. B. 1881. A synopsis of the New Zealand species of *Veronica*, Linn., with notes on new species. *Trans. New Zealand Inst. Technol.* 13: 344–359.
- Baltisberger, M. 1988. Chromosomenzahlen einiger Pflanzen aus Albanien. II. *Ber. Geobot. Inst. ETH Stiftung Rübel* 54: 42–50.
- Bayly, M. J. & A. V. Kellow. 2006. *New Zealand Hebes*, an Illustrated Guide. Te Papa Press, Wellington, New Zealand.
- Bell, C. R. 1965. Documented plant chromosome numbers. *Sida* 2: 168–170.
- Bennett, M. D. 1972. Nuclear DNA content and minimum generation time in herbaceous plants. *Proc. Roy. Soc. Lond., Ser. B., Biol. Sci.* 181: 109–135.
- Böcher, T. W. 1944. The leaf size of *Veronica officinalis* in relation to genetic and environmental factors. *Dansk Bot. Ark.* 11: 1–20.
- Borgmann, E. 1964. Anteil der Polyploiden in der Flora des Bismarckgebirges von Ostneuguinea. *Z. Bot.* 52: 118–172.
- Borhidi, A. 1968. Karyological studies on southeast European plant species, I. *Acta Bot. Acad. Sci. Hung.* 14: 253–260.

- Borissova, A. G. 1955. *Veronica*. Pp. 373–557 in B. K. Shishkin & E. G. Bobrov (editors), *Flora SSSR*, Vol. 22. Akademii Nauk SSSR, Moskva, Leningrad.
- Bousquet, J., S. H. Strauss, A. H. Doerksen & R. A. Price. 1992. Extensive variation in evolutionary rate of *rbcL* gene sequences among seed plants. *Proc. Natl. Acad. Sci. U.S.A.* 89: 7844–7848.
- Brandt, J.-P. 1952. Contribution à la cytologie du genre *Veronica*. *Bull. Soc. Neuchâteloise Sci. Nat.* 75: 179–188.
- . 1961. Cytotaxinomie et cytogéographie de *Veronica prostata* L. *Bull. Soc. Neuchâteloise Sci. Nat.* 84: 35–88.
- Briggs, B. G. & F. Ehrendorfer. 2006. Chromosome numbers of Australian and New Guinean species of *Veronica* (Plantaginaceae). *Telopea* 11: 294–298.
- Chuang, T. I. & L. R. Heckard. 1992. Chromosome numbers of some North American Scrophulariaceae, mostly Californian. *Madroño* 39: 137–149.
- Davlianidze, M. 1980. Numeri chromosomatum nonnularum plantarum caucasicarum. *Zametki Sist. Geogr. Rast.* 36: 75–76.
- de Jongh, S. E. & J. H. Kern. 1973. De variabiliteit van *Veronica hederifolia* L. in Nederland. *Gorteria* 6: 202–203.
- Dobeš, C. & E. Vitek. 2000. Documented chromosome number checklist of Austrian vascular plants. *Verlag des Naturhistorischen Museums Wien*, Wien.
- Dzhus, M. A. & S. A. Dmitrieva. 2001. Hromosomnye čisla vidov roda *Veronica* (Scrophulariaceae) v Belorussii (Chromosome numbers in the species of the genus *Veronica* (Scrophulariaceae) from Byelorussia). *Bot. Zhurn.* 86: 144–147.
- Ferrarella, A., F. Grisafi, F. Lentini & M. R. Melati. 1981. Numeri cromosomici per la flora italiana. *Inform. Bot. Ital.* 13: 189–194.
- Fischer, M. A. 1967. Beiträge zur Cytotaxonomie der *Veronica hederifolia*-Gruppe (Scrophulariaceae). *Österr. Bot. Z.* 114: 189–233.
- . 1969. Einige Chromosomenzahlen aus den Gattungen *Veronica*, *Pseudolysimachion*, *Paederota*, *Wulfenia* und *Lagotis* (Scrophulariaceae–Veronicinae). *Österr. Bot. Z.* 116: 430–443.
- . 1970. Zur Cytotaxonomie der Verwandtschaftsgruppe um *Veronica orientalis* Mill., emend. Ait. in der Türkei. *Österr. Bot. Z.* 118: 131–161.
- . 1972. Neue Taxa, Chromosomenzahlen und Systematik von *Veronica* subsect. *Acinifolia* (Römpf) Stroh. *Österr. Bot. Z.* 121: 413–437.
- . 1973. Notizen zur Systematik, Chromosomenzahl und Verbreitung einiger *Veronica*-Sippen in Kärnten. *Carinthia* 83: 379–388.
- . 1975a. Untersuchungen über den Polyploidkomplex *Veronica cymbalaria* agg. (Scrophulariaceae). *Pl. Syst. Evol.* 123: 97–105.
- . 1975b. The *Veronica hederifolia* group: Taxonomy, ecology, and phylogeny. Pp. 48–60 in S. M. Walter (editor), *European Floristic and Taxonomic Studies*. Bot. Soc. Brit. Is. Conf. Rep. 15.
- . 1978. *Veronica* L. Pp. 689–753 in P. H. Davis (editor), *Flora of Turkey*, Vol. 6. University Press, Edinburgh.
- . 1981. *Veronica*. Pp. 52–165 in K. H. Rechinger (editor), *Flora Iranica*, Vol. 147. Akademische Druck- und Verlagsanstalt, Graz.
- . 1984. Zur Chorologie und Systematik der *Veronica hederifolia*-Gruppe in Jugoslawien. *Akad. Nauka i Umjetn. Bosne i Hercegov. Radovi* 76, Odjelj. Prir. i Mat. N. 23: 55–77.
- , V. Veljović & B. Tatić. 1984. *Veronica scardica*—A neglected species of the Serbian Flora. *Glas. Inst. Bot. Bašte Univ. Beogr.* 18: 37–52.
- Fukui, K. & S. Nakayama. 1996. *Plant Chromosomes. Laboratory Methods*. CRC Press, Boca Raton, Florida.
- Gadella, T. W. J. & E. Kliphuis. 1963. Chromosome numbers of flowering plants in the Netherlands. *Acta Bot. Neerl.* 12: 195–230.
- & ———. 1966. Chromosome numbers of flowering plants in the Netherlands II. *Proc. Kon. Ned. Akad. Wetensch. C.* 69: 541–556.
- & ———. 1976. Some critical remarks on *Veronica hederifolia* L. in the Netherlands. *Proc. Kon. Ned. Akad. Wetensch. C.* 79: 61–73.
- Garnock-Jones, P. J. & D. G. Lloyd. 2004. A taxonomic revision of *Parahebe* (Scrophulariaceae–Antirrhinoideae) in New Zealand. *New Zealand J. Bot.* 42: 181–232.
- , D. C. Albach & B. Briggs. 2007. Botanical names in Southern Hemisphere *Veronica* (Plantaginaceae): Sect. *Derwentia*, sect. *Detzneria*, and sect. *Hebe*. *Taxon* 56: 571–582.
- Goldblatt, P. & D. E. Johnson. 2006. Index to Plant Chromosome Numbers 2001–2003. *Monogr. Syst. Bot. Missouri Bot. Gard.* 106.
- Graze, H. 1935. Weitere Chromosomenuntersuchungen bei *Veronica*-Arten der Sektion *Pseudolysimachia* Koch. *Jahrb. Wiss. Bot.* 81: 609–662.
- Gukasian, A. G. & A. B. Safarian. 1990. Chromosome numbers of some representatives of the Armenian Flora. *Biol. Zhurn. Armenii* 43: 259–260.
- Guo, S. & X.-Z. Liu. 2001. The chromosome number of *Veronica hederifolia* L. in China and its ecological significance. *Guihaia* 21: 111–112.
- Gurzenkov, N. N. 1973. Studies of chromosome numbers of plants from the south of the Soviet Far East. *Komarovskie Ctenija* 20: 47–62.
- Harvey, P. H. & A. Rambaut. 1998. Phylogenetic extinction rates and comparative methodology. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 265: 1691–1696.
- Heitz, E. 1926. Der Nachweis der Chromosomen. Vergleichende Studien über ihre Zahl, Größe und Form im Pflanzenreich I. *Z. Bot.* 18: 625–681.
- Hofelich, A. 1935. Die Sektion *Alsinebe* Griseb. der Gattung *Veronica* in ihren chromosomalen Grundlagen. *Jahrb. Wiss. Bot.* 81: 541–572.
- Hong, D. & M. A. Fischer. 1998. *Veronica*. Pp. 65–80 in Z.-Y. P. R. Wu (editor), *Flora of China*, Vol. 18. Science Press, Beijing, and Missouri Botanical Garden Press, St. Louis.
- Hong, D.-Y. 1984. Taxonomy and evolution of the Veroniceae (Scrophulariaceae) with special reference to palynology. *Opera Bot.* 75: 5–60.
- Huang, R., S. Shen & X. Lu. 1996. Studies of the chromosome numbers and polyploidy for some plant in the north-east Qinghai-Xizang plateau. *Acta Bot. Boreal.-Occid. Sin.* 16: 310–318.
- Huber, A. 1927. Beiträge zur Klärung verwandtschaftlicher Beziehungen in der Gattung *Veronica*. I. Die Kernuntersuchungen in der Gattung *Veronica*. *Jahrb. Wiss. Bot.* 66: 359–380.
- Hultén, E. 1930. Flora of Kamtchatka and the adjacent islands. IV Dicotyledonae Pyrolaceae Compositae. *Kungl. Svenska Vetenskapsakad. Handl., ser. 3*, 8: no. 2.
- Kemularia-Nathadze, L. 1955. Generum Scrophulariae L. et Veronicae L. species novae. *Zametki Sist. Geogr. Rast.* 18: 48–57.

- Khatoon, S. & S. I. Ali. 1993. Chromosome Atlas of the Angiosperms of Pakistan. Department of Botany, University of Karachi, Karachi, Pakistan.
- Kliphuis, E. & J. H. Wieffering. 1972. Chromosome numbers of some angiosperms from the south of France. *Acta Bot. Neerl.* 21: 598–604.
- Knaben, G. & T. Engelskjön. 1967. Chromosome numbers of Scandinavian arctic-alpine plant species. II. *Acta Boreal.*, A. 21: 1–57.
- Krogulevich, R. E. & T. S. Rostovtseva. 1984. Chromosome numbers of flowering plants of Siberia and the Far East. *Akad. Nauk SSSR Sibirskoe, Novosibirsk.*
- Küpfer, P. 1968. Nouvelles prospections caryologiques dans la flore orophile des Pyrénées et de la Sierra Nevada. *Bull. Soc. Neuchâteloise Sci. Nat.* 91: 87–104.
- . 1969. Recherches cytotoxonomiques sur la flore des montagnes de la péninsule ibérique. *Bull. Soc. Neuchâteloise Sci. Nat.* 92: 31–48.
- . 1972. Cytotaxonomie et cytogéographie de quelques groupes d'orophytes du bassin occidental de la Méditerranée et des Alpes. *Compt. Rend. Hebd. Séances Acad. Sci.* 275: 1753–1756.
- . 1974. Recherches sur les liens de parenté entre la flore orophile des Alpes et celle des Pyrénées. *Boissiera* 23: 1–315.
- La Cour, L. F. 1954. Smear and squash techniques in plant cytology. *Lab. Practique* 3: 326–330.
- Lehmann, E. 1910. Über Merkmalseinheiten in der *Veronica*-Sektion *Alsinebe*. *Z. Bot.* 2: 577–602.
- . 1940. Polyploidie und geographische Verbreitung der Arten der Gattung *Veronica*. *Jahrb. Wiss. Bot.* 89: 461–542.
- Lepper, L. 1964. Die Cytotaxonomie der Gattung *Wulfenia* Jacq.—ein Beitrag zum Kleistoploidieproblem. Ph.D. thesis, Friedrich-Schiller-Universität, Jena.
- Levin, D. A. 2002. The Role of Chromosomal Change in Plant Evolution. Oxford University Press, New York.
- Lippert, W. & G. R. Heubl. 1989. Chromosomenzahlen von Pflanzen aus Bayern und angrenzenden Gebieten. *Ber. Bayer. Bot. Ges.* 60: 73–83.
- Lökvist, B. & U.-M. Hultgård. 1999. Chromosome numbers in South Swedish vascular plants. *Opera Bot.* 137: 1–42.
- Löve, A. & D. Löve. 1956. Cytotaxonomical conspectus of the Icelandic flora. *Acta Horti Gothob.* 20: 65–291.
- . 1972a. IOPB Chromosome number reports XXXVI. *Taxon* 21: 333–346.
- . 1972b. IOPB Chromosome number reports XXXVII. *Taxon* 21: 495–500.
- . 1978. IOPB Chromosome number reports LX. *Taxon* 27: 223–231.
- . 1979. IOPB Chromosome number reports LXIV. *Taxon* 28: 391–408.
- . 1981. IOPB Chromosome number reports LXXIII. *Taxon* 30: 829–861.
- . 1982. IOPB Chromosome number reports LXXVI. *Taxon* 31: 574–598.
- . 1985. Chromosome number reports LXXXVI. *Taxon* 34: 159–164.
- . 1986a. Chromosome number reports XCI. *Taxon* 35: 404–410.
- . 1986b. Chromosome number reports XCIII. *Taxon* 35: 897–903.
- Magulaev, A. Y. 1984. Cytotaxonomic study in some flowering plants of the North Caucasus. *Bot. Zhurn.* 69: 511–517.
- Marchant, N. G. 1970. Experimental Taxonomy of *Veronica* section *Beccabunga* Griseb. Ph.D. thesis, University of Cambridge, Cambridge.
- Martínez-Ortega, M. M., J. A. Sánchez-Agudo & E. Rico. *Veronica*. In C. Benedí, E. Rico, J. Güemes & A. Herrero (editors), *Flora Iberica*, Vol. 13. Real Jardín Botánico de Madrid, CSIC, Madrid (in press).
- Meškova, L. Z. 1965. Primenenie kariologiceskogo isledovaniya k sistematike roda *Veronica* L. Avtoref. Kand. Diss. Kazan., 1–16.
- Muñoz-Centeno, L. M., D. C. Albach, J. A. Sánchez-Agudo & M. M. Martínez-Ortega. 2006. Systematic significance of seed morphology in *Veronica* (Plantaginaceae). A phylogenetic perspective. *Ann. Bot. (London)* 98: 335–350.
- , L. Delgado-Sánchez, M. Santos-Vicente & M. M. Martínez-Ortega. 2007. Taxonomy of *Veronica* L. subsect. *Veronica* (Plantaginaceae) in the western Mediterranean. *Bot. J. Linn. Soc.* 155: 65–81.
- Nilsson, Ö. & P. Lassen. 1971. Chromosome numbers of vascular plants from Austria, Mallorca and Yugoslavia. *Bot. Not.* 124: 270–276.
- Nordenstam, B. & Ö. Nilsson. 1969. Taxonomy and distribution of *Veronica hederifolia* s. lat. (Scrophulariaceae) in Scandinavia. *Bot. Not.* 122: 233–247.
- Öztürk, A. & M. A. Fischer. 1982. Karyosystematics of *Veronica* sect. *Beccabunga* (Scrophulariaceae) with special reference to the taxa in Turkey. *Pl. Syst. Evol.* 140: 307–319.
- Pazy, B. 2000. Flora Palaestina: Chromosome numbers. *Israel J. Pl. Sci.* 48: 7–32.
- Peev, D. 1975. Genus *Veronica* in Bulgaria—Some new taxa and chromosome numbers. *Phytology* 2: 42–46.
- Peev, R. 1972. New taxa and ploidy levels of some Bulgarian *Veronica* species. *Compt. Rend. Acad. Bulg. Sci.* 25: 811–814.
- Podlech, D. 1986. Chromosomenstudien an Pflanzen des Saharo-Sindischen Trockengebietes. *Mitt. Bot. Staats-samml. München* 22: 5–20.
- & A. Dieterle. 1969. Chromosomenstudien an afghanischen Pflanzen. *Candollea* 24: 185–243.
- Pouzar, Z. 1964. Nomenclatural remarks on some generic names of phanerogams validly published by Filip Maximilian Opiz. *Preslia* 36: 337–342.
- Probatova, N. S. & A. P. Sokolovskaya. 1990. Chromosome numbers in some representatives of the families Asclepiadaceae, Asteraceae, Boraginaceae, Chenopodiaceae, Lamiaceae, Oleaceae, Onagraceae, Scrophulariaceae, Solanaceae, Urticaceae from the Soviet Far East. *Bot. Zhurn.* 75: 1619–1622.
- , E. G. Rudyka & A. P. Sokolovskaya. 1996. Chromosome numbers in synanthropic plants from the Russian Far East. *Bot. Zhurn.* 81: 98–101.
- Römpf, H. 1928. Die Verwandtschaftsverhältnisse in der Gattung *Veronica*. *Repert. Spec. Nov. Regni Veg. Beih.* 50: 1–171.
- Rossitto, M., D. Ottonello & S. Fici. 1983. Numeri cromosomici per la Flora Italiana: 993–1002. *Inform. Bot. Ital.* 15: 188–194.
- Saeidi-Mehrvarz, S. & A. Kharabian. 2005. Chromosome counts of some *Veronica* (Scrophulariaceae) species from Iran. *Turkish J. Bot.* 29: 263–267.
- Skalinska, M. 1964. Additions to chromosome numbers of Polish angiosperms (fifth contribution). *Acta Soc. Bot. Poloniae* 33: 45–77.
- Sorsa, V. 1963. Chromosomenzahlen finnischer Kormophyten. II. *Ann. Acad. Sci. Fenn., Ser. A, IV, Biol.* 68: 1–14.
- Stepanov, N. V. 1994. Chromosome numbers in some nemoral species of the west Sayan (Krasnoyarsk region). *Bot. Zhurn.* 79: 125–128.

Tischler, G. 1950. Die Chromosomenzahlen der Gefäßpflanzen Mitteleuropas. Dr. W. Junk, 's-Gravenhage.

Travniček, B., M. A. Lysák, J. Cíhalíková & J. Dolezel. 2004. Karyo-taxonomic study of the genus *Pseudolysimachion* (Scrophulariaceae) in the Czech Republic and Slovakia. *Folia Geobot. Phytotax.* 39: 173–203.

Tumadjanov, I. I. & R. K. Beridze. 1969. On the speciation within the series *gentianoides* Boriss. of the genus *Veronica* L. *Bot. Zhurn.* 54: 1647–1660.

———, ——— & A. I. Pogosyan. 1972. Experience in analysis of *Veronica gentianoides* Vahl s. l. populations along the profile of the Minor Caucasus mountains. *Bot. Zhurn.* 57: 1495–1515.

———, ——— & ———. 1977. Populational structure, phylogenetic relationships and origin of polyploid complex *Veronica gentianoides* Vahl aggr. (Scrophulariaceae). *Bot. Zhurn.* 62: 1548–1559.

Vasudevan, K. N. 1975. Contribution to the cytotaxonomy and cytogeography of the Flora of the Western Himalayas (with an attempt to compare it with the Flora of the Alps). Part II. *Ber. Schweiz. Bot. Ges.* 85: 210–252.

Wagstaff, S. J. & P. J. Garnock-Jones. 1998. Evolution and biogeography of the *Hebe* complex (Scrophulariaceae) inferred from ITS sequences. *New Zealand J. Bot.* 36: 425–437.

———, M. J. Bayly, P. J. Garnock-Jones & D. C. Albach. 2002. Classification, origin, and diversification of the New Zealand Hebes (Scrophulariaceae). *Ann. Missouri Bot. Gard.* 89: 38–63.

Weiss, H., B.-Y. Sun, T. F. Stuessy, C. H. Kim, H. Kato & M. Wakabayashi. 2002. Karyology of plant species endemic to Ullung Island (Korea) and selected relatives in peninsular Korea and Japan. *Bot. J. Linn. Soc.* 138: 93–105.

APPENDIX I. List of all species in the Veroniceae for which chromosome numbers are known. Chromosome numbers are expressed as $2n$ values and x refers to the ploidy level. Subscripts (x_{Vst} , x_{Pic} , x_{Psl} , x_{Hebe}) refer to the fact that these groups have a different chromosome base number because they are themselves derived from a polyploidization event. The list follows the classification of the tribe as outlined in Albach et al. (2004b) and Garnock-Jones et al. (2007).

Lagotis Gaertn.

$x = 11$

- L. brevituba* Maxim., ? $x = 54$
- L. cashmeriana* (Royle) Rupr., $2x = 22$
- L. glauca* Gaertn., $2x = 22$
- L. integrifolia* (Willd.) Schischk., $4x = (43) 44$
- L. minor* (Willd.) Standl., $2x, 4x = 22, 44$
- L. stolonifera* (K. Koch) Maxim., $2x = 22$
- L. takedana* Miyabe & Tatew., $2x = 22$

Species not investigated: *Lagotis alutacea* W. W. Sm., *L. angustibracteata* P. C. Tsoong & H. P. Yang, *L. brachystachya* Maxim., *L. chumbica* R. R. Mill, *L. clarkei* Hook. f., *L. crassifolia* Prain, *L. decumbens* Rupr., *L. globosa* (Kurz) Hook. f., *L. gregorjevi* Krassn., *L. hultenii* Polunin, *L. humilis* P. C. Tsoong & H. P. Yang, *L. ikonnikovii* Schischk., *L. integra* W. W. Sm., *L. kongboensis* T. Yamaz., *L. korolkowii* (Regel & Schmalh.) Maxim., *L. kunawurensis* (Royle ex Benth.) Rupr., *L. macrosiphon* P. C. Tsoong & H. P. Yang, *L. nepalensis* T. Yamaz., *L. pharica* Prain, *L. praecox* W. W. Sm., *L. ramalana* Batalin, *L. spectabilis* (Kurz) Hook. f., *L.*

uralensis Schischk., *L. wardii* W. W. Sm., *L. yesoensis* Tatew., *L. yunnanensis* W. W. Sm.

Wulfenia Jacq.

$x = 9$

- W. baldacii* Degen, $2x = 18$
- W. bleicicii* Lakušić, $2x = 18$
- W. carinthiaca* Jacq., $2x = 18$
- W. orientalis* Boiss., $2x = 18$

Paederota L.

$x = 9$

- P. bonarota* L., $4x = 36$
- P. lutea* Scop., $4x, 6x = 36, 54$
- P. ×churchillii* Huter, $4x = 36$

Wulfeniopsis D. Y. Hong

$x = 8$

- W. amherstiana* (Benth.) D. Y. Hong, $2x, 4x = 16, 32$
- W. nepalensis* (T. Yamaz.) D. Y. Hong, $2x = 16$

Veronicastrum Heist. ex Fabr.

$x = 17$ (8 + 9; see Albach & Chase, 2004)

- V. brunonianum* (Benth.) D. Y. Hong, $2x_{Vst} = 34$
- V. japonicum* (Nakai) T. Yamaz., $2x_{Vst} = 34$
- V. liukiunense* (Ohwi) T. Yamaz., $8x_{Vst} = 136$
- V. sibiricum* (L.) Pennell, $2x_{Vst} = 34$
- V. villosulum* (Miq.) T. Yamaz., $4x_{Vst} = 68$
- V. virginicum* Farw., $2x_{Vst} = 34$

Species not investigated: *Veronicastrum axillare* (Siebold & Zucc.) T. Yamaz., *V. caulopterum* (Hance) T. Yamaz., *V. formosanum* (Masam.) T. Yamaz., *V. kitamurae* (Ohwi) T. Yamaz., *V. latifolium* (Hemsl.) T. Yamaz., *V. longispicatum* (Merr.) T. Yamaz., *V. rhombifolium* (Hand.-Mazz.) P. C. Tsoong, *V. robustum* (Diels) D. Y. Hong, *V. stenostachyum* (Hemsl.) T. Yamaz., *V. tagawae* (Ohwi) T. Yamaz., *V. tubiflorum* (Fisch. & C. A. Mey.) H. Hara, *V. yunnanense* (W. W. Sm.) T. Yamaz.

Picrorhiza Royle ex Benth.

$x = 17$ (8 + 9; see Albach & Chase, 2004)

- P. kurrooa* Royle ex Benth., $4x_{Pic} = 34$

Species not investigated: *Picrorhiza scrophulariiflora* Pennell, *Neopicrorhiza minima* R. R. Mill.

Veronica L.

I. Veronica subgen. Veronica

- 1. *Veronica* sect. *Glandulosae* (Römpf) Albach
 - 1a. *Veronica* subsect. *Glandulosae* (Römpf) Stroh

$x = 8$ (?), 9

- V. abyssinica* Fresen., $6x = 48$
- V. glandulosa* subsp. *mannii* (Hook. f.) Elenevsky, $6x = 54$
- V. gunae* Schweinf. ex Engl., $6x = 54$

2. *Veronica* sect. *Scutellatae* G. Don

- 2a. *Veronica* subsect. *Scutellatae* Benth.

$x = 9$

- V. scutellata* L., $2x = 18$

3. *Veronica* sect. *Montanae* (Boriss. ex Elenevsky) Assejeva

- 3a. *Veronica* subsect. *Canae* (T. Yamaz.) Elenevsky
 $x = 7, 8, ?$
V. cana Wall., $?x = 50, 52$
V. henryi T. Yamaz., $4x = 32$
V. miqueliana Nakai, $6x = 48$
V. robusta (Prain) T. Yamaz., $6x = 42$

Species not investigated: *Veronica chayuensis* D. Y. Hong, *V. deltigera* Wall. ex Benth., *V. fargesii* Franch., *V. forrestii* Diels, *V. japonensis* Makino, *V. laxissima* D. Y. Hong, *V. longipetiolata* D. Y. Hong, *V. muratae* T. Yamaz., *V. oligosperma* Hayata, *V. piroliformis* Franch., *V. riae* H. J. P. Winkl., *V. sutchuensis* Franch., *V. szechuanica* Batalin, *V. taiwanica* T. Yamaz., *V. tibetica* D. Y. Hong, *V. tsinglingensis* D. Y. Hong, *V. vandellioides* Maxim., *V. yunnanensis* D. Y. Hong.

- 3b. *Veronica* subsect. *Montanae* Boriss. ex Elenevsky
 $x = 9$
V. montana L., $2x, 4x = 18, 36$

4. *Veronica* sect. *Veronica* L.
4a. *Veronica* subsect. *Alpinae* Benth.

- $x = 9$
V. alpina L., $2x = 18$
V. bellidioides L., $2x, 4x = 18, 36$
V. copelandii Eastw., $2x = 18$
V. cusickii A. Gray, $2x, 8x = 18, 72$
V. nipponica Makino, $2x = 18$
V. nutans Bong., $2x = 18$
V. stelleri Pall. ex Link, $2x = 18$
V. wormskjoldii Roem. & Schult., $4x = 36$

- 4b. *Veronica* subsect. *Gouani* (Römpf) Stroh
 $x = 9$
V. ponae Gouan, $6x = 54$

- 4c. *Veronica* subsect. *Urticifoliae* Boriss. ex Elenevsky
 $x = 9$
V. urticifolia Jacq., $2x = 18$

- 4d. *Veronica* subsect. *Veronica*
 $x = 9$
V. allionii Vill., $2x = 18$
V. officinalis L., $2x, 4x = 18, 36$
V. onoei Franch. & Sav., $4x = 36$
V. ×tournefortii (Vill.) F. W. Schmidt, $3x = 27$
(= *V. allionii* × *V. officinalis*)

Species not investigated: *Veronica dabneyi* Hochst., *V. morrisonicola* Hayata.

- 4e. *Veronica* subsect. *Aphyllae* (Römpf) Stroh
 $x = 9$
V. aphylla L., $2x = 18$
V. grandiflora Gaertn., $?x = 48-50$

- 4f. *Veronica* subsect. *Carpathicae* Elenevsky
 $x = 7$
V. baumgartenii Roem. & Schult., $2x = 14$

II. *Veronica* subgen. *Beccabunga* (Hill) M. M. Mart. Ort., Albach & M. A. Fisch.
Incertae sedis
 $x = 9$

- V. hispidula* Boiss. & Huet., $2x, 4x = 18, 36$

1. *Veronica* sect. *Beccabunga* (Hill) Dumort.

- 1a. *Veronica* subsect. *Beccabunga* (Hill) Elenevsky
 $x = 9$

- V. americana* Schwein. ex Benth., $4x = 36$
V. beccabunga L. subsp. *beccabunga*, $2x, 4x = 18, 36$
V. beccabunga subsp. *abscondita* M. A. Fisch., $2x = 18$
V. beccabunga subsp. *muscosa* (Korsh.) Elenevsky, $2x = 18$

- 1b. *Veronica* subsect. ined.

- $x = 9$
V. anagallis-aquatica L., $4x = 36$
V. anagalloides Guss. subsp. *anagalloides*, $2x, 4x = 18, 36$
V. anagalloides subsp. *heureka* M. A. Fisch., $2x, 4x = 18, 36$
V. catenata Pennell, $4x = 36$
V. lysimachioides Boiss., $2x = 18$
V. michauxii Lam., $4x = 36$
V. oxycarpa Boiss., $2x, 4x = 18, 36$
V. poljensis Murb., $4x = 36$
V. scardica Griseb., $2x, 4x = 18, 36$
V. spec. indet. aff. "beccabungoides," $4x = 36$
V. undulata Wall., $6x = 54$
V. ×myriantha Tosh. Tanaka, $5x = 45$
V. anagallis-aquatica × *V. michauxii*, $4x = 36$

Species not investigated: *Veronica kaiseri* Täckh.

- 1c. *Veronica* subsect. *Peregrinae* Elenevsky
 $x = 9$
Veronica peregrina L., $6x (-2) = 52$

2. *Veronica* sect. *Acinifolia* (Römpf) Albach

- 2a. *Veronica* subsect. *Acinifolia* (Römpf) Stroh

- $x = 7$
V. acinifolia L., $2x = 14$
V. bozakmanii M. A. Fisch., $4x = 28$
V. pusilla Kotschy & Boiss., $2x = 14$
V. reuteriana Boiss., $4x, 6x = 28, 42$
V. syriaca Roem. & Schult., $2x = 14$

Species not investigated: *Veronica balansae* Stroh, *V. debilis* Freyn, *V. oetaea* Gustavsson, *V. yildirimlii* Öztürk.

3. *Veronica* sect. *Serpyllifolia* G. Don

- 3a. *Veronica* subsect. *Gentianoides* (G. Don) Assejeva

- $x = 8$ (?)
V. gentianoides Vahl, $2-10x = 16, 24, 32, 36, 40, 48, 56, 64, 72, 80$
V. schistosa E. Busch, $3x, 6x = 24, 48$
Species not investigated: *Veronica kopgeciensis* Öztürk & M. A. Fisch.

- 3b. *Veronica* subsect. *Serpyllifolia* (G. Don) Stroh

- $x = 7$
V. nevadensis (Pau) Pau var. *nevadensis*, $2x = 14$
V. nevadensis var. *langei* (Lacaita) M. M. Mart. Ort. & E. Rico, $2x = 14$
V. serpyllifolia L. subsp. *serpyllifolia*, $2x, 4x = 14, 28$
V. serpyllifolia subsp. *repens* (Clarion ex DC.) Hartl in Hegi, $2x = 14$

Species not investigated: *Veronica archboldii* Pennell, *V. platycarpa* Pennell.

3c. *Veronica* subsect. *Telephiifolia* M. M. Mart. Ort. & E. Rico

$x = 7$
V. telephiifolia Vahl, $2x = 14$

Species not investigated: *Veronica daranica* Saeidi & Ghahr., *V. davisii* M. A. Fisch.

III. *Veronica* subg. *Pseudolysimachium* (Opiz) Buchenau

1. *Veronica* sect. *Schmidtianae* (Boriss. ex. T. Yamaz.) Assejeva

1a. *Veronica* subsect. *Schmidtiana* Boriss. ex Elenevsky
 $x_{psl} = 17$ ($9 + 9 - 1$)
V. nakaiana Ohwi, $2x = 34$
V. schmidtiana Regel, $2x = 34$

2. *Veronica* sect. *Pseudolysimachium* W. D. J. Koch
 2a. *Veronica* subsect. *Alatavicae* Boriss. ex Elenevsky

Species not investigated: *Veronica alatavica* Popov, *V. qingheensis* Y. Z. Zhao.

2b. *Veronica* subsect. *Dahuricae* (Holub) Elenevsky
 $x_{psl} = 17$ ($9 + 9 - 1$)
V. daurica Steven, $2 x_{psl} = 34$ (printing error?)
V. olgensis Kom., $2 x_{psl} = 24$

Species not investigated: *Veronica ogurae* (T. Yamaz.) Albach, *V. pyrethrina* Nakai.

2c. *Veronica* subsect. *Pinnatae* (Holub) Elenevsky
 $x_{psl} = 17$ ($9 + 9 - 1$)
V. pinnata L., $2 x_{psl} = 34$

Species not investigated: *Veronica laeta* Kar. & Kir., *V. sessiliflora* Bunge ex Ledeb.

2d. *Veronica* subsect. *Longifoliae* (Holub) Elenevsky
 $x_{psl} = 17$ ($9 + 9 - 1$)
V. bachofenii Heuff., $2 x_{psl} = 34$
V. kiusiana subsp. *maritima* (Nakai) T. Yamaz., $4 x_{psl} = 68$
V. kiusiana subsp. *miyabei* (Nakai & Hondo) T. Yamaz., $2 x_{psl} = 34$
V. longifolia L., $2 x_{psl}$, $4 x_{psl} = 34$, 68
V. subsessilis (Miq.) Carriere, $4 x_{psl} = 68$

Species not investigated: *Veronica ovata* Nakai, *V. sachalinensis* T. Yamaz., *V. sajanensis* Printz, *V. sieboldiana* Miq., *V. taigischensis* Stepanov.

2e. *Veronica* subsect. *Pseudolysimachium* (W. D. J. Koch) Elenevsky
 $x_{psl} = 17$ ($9 + 9 - 1$)
V. barrelieri H. Schott ex Roem. & Schult. subsp. *barrelieri*, $2 x_{psl}$, $4 x_{psl} = 34$, 68
V. barrelieri subsp. *crassifolia* Wierzb., $4 x_{psl} = 68$
V. barrelieri subsp. *prodanii* (Degen) Albach, $4 x_{psl} = 68$
V. incana L., $4 x_{psl} = 68$
V. incana subsp. *incana*, $2 x_{psl} = 34$
V. incana subsp. *pallens* (Host) Albach, $4 x_{psl} = 68$
V. orchidea Crantz, $2 x_{psl}$, $4 x_{psl} = 34$, 68
V. ornata Monjuschko, $4 x_{psl} = 68$

V. porphyriana Pavlov, $2 x_{psl}$ (flow cytometry)
V. spicata L. subsp. *spicata*, $2 x_{psl}$, $4 x_{psl} = 34$, 68
V. spicata subsp. *euxina* (Turrill) Stoj. & Stef., $2 x_{psl} = 34$
V. spicata subsp. *fischeri* Trávn., $4 x_{psl} = 68$
V. spicata subsp. *lanisepala* (Trávn.) Albach, $2 x_{psl} = 34$

2f. *Veronica* subsect. *Spuriae* (Holub) Elenevsky
 $x_{psl} = 17$ ($9 + 9 - 1$)
V. liniariifolia Pall. ex Link, $2 x_{psl} = 34$
V. rotunda Nakai, $2 x_{psl} = 34$
V. spuria L., $2 x_{psl}$, $4 x_{psl} = 34$, 68

IV. *Veronica* subg. *Synthyris* (Benth.) M. M. Mart. Ort., Albach & M. A. Fisch.

$x = 12$
V. alaskensis M. M. Mart. Ort. & Albach, $2x = 24$
V. besseyi M. M. Mart. Ort. & Albach, $2x = 24$
V. bullii (Eaton) M. M. Mart. Ort. & Albach, $2x = 24$
V. californica M. M. Mart. Ort. & Albach, $2x = 24$
V. canbyi (Pennell) M. M. Mart. Ort. & Albach, $4x = 48$
V. dissecta (Rydb.) M. M. Mart. Ort. & Albach, $2x = 24$
V. idahoensis M. M. Mart. Ort. & Albach, $2x = 24$
V. missurica Raf. subsp. *missurica*, $2x = 24$
V. missurica subsp. *major* (Hook.) M. M. Mart. Ort. & Albach, $2x$, $4x = 24$, 48
V. missurica subsp. *stellata* (Pennell) M. M. Mart. Ort. & Albach, $2x$, $4x = 24$, 48
V. oblongifolia (Pennell) M. M. Mart. Ort. & Albach, $2x = 24$
V. paysonii (Pennell & L. O. Williams) M. M. Mart. Ort. & Albach, $2x = 24$
V. plantaginea E. James, $2x$, $4x = 24$, 48
V. ranunculina (Pennell) M. M. Mart. Ort. & Albach, $2x = 24$
V. regina-nivalis M. M. Mart. Ort. & Albach, $2x = 24$
V. ritteriana (Eastw.) M. M. Mart. Ort. & Albach, $4x = 48$
V. rubra (Douglas) M. M. Mart. Ort. & Albach, $2x = 24$
V. schizantha (Piper) M. M. Mart. Ort. & Albach, $2x = 24$
V. utahensis M. M. Mart. Ort. & Albach, $2x = 24$
V. wyomingensis (A. Nelson) M. M. Mart. Ort. & Albach, $2x$, $4x = 24$, 48
V. missurica $\times$ *V. rubra*, $2x = 24$

V. *Veronica* subg. *Cochlidiosperma* (Rehb.) M. M. Mart. Ort. & Albach

1. *Veronica* sect. *Diplophyllum* (Lehm.) Boriss.
 $x = 9$
V. crista-galli Steven, $2x = 18$

Species not investigated: *Veronica simensis* Fresen.

2. *Veronica* sect. *Cochlidiosperma* (Rehb.) Benth.
 2a. *Veronica* subsect. *Cymbalariae* Benth.
 $x = 9$
V. cymbalaria Bodard, $4x$, $6x = 36$, 54
V. lycica E. B. J. Lehm., $2x = 18$
V. panormitana Tineo, $2x = 18$
V. stamatiadae M. A. Fisch. & Greuter, $2x = 18$
V. trichadena Jord. & Fourr., $2x$, $4x = 18$, 36

2b. *Veronica* subsect. *Cochlidiosperma* (Rehb.) Albach
 $x = 9$, ?
V. sibthorpioides Deb., Degen & Hervier, $?x = 28$, 30
V. hederifolia L., $6x = 54$
V. stewartii Pennell, $2x = 18$
V. sublobata M. A. Fisch., $4x = 36$
V. triloba Opiz, $2x = 18$

VI. *Veronica* subg. *Pellidosperma* (E. B. J. Lehm.) M. M. Mart. Ort., Albach & M. A. Fisch.

$x = 7, 8, 9$

V. glauca Sibth. & Sm. subsp. *glauca*, $2x = 18$

V. glauca subsp. *chaubardii* (Boiss. & Reut.) Maire & Petitm., $2x = 18$

V. glauca subsp. *peloponnesiaca* (Boiss. & Orph.) Maire & Petitm., $2x = 18$

V. mazanderanae Wendelbo, $2x = 16$

V. praecox All., $2x = 18$

V. triphyllus L., $2x = 14$

Species not investigated: *Veronica aznavourii* Dörfl., *V. donii* Römpp, *V. samuelssonii* Rech. f.

VII. *Veronica* subg. *Stenocarpon* (Boriss.) M. M. Mart. Ort., Albach & M. A. Fisch.

$x = 8$

V. ciliata Fisch. subsp. *ciliata*, $2x = 16$

V. ciliata subsp. *cephaloides* (Pennell) D. Y. Hong, $2x = 16$

V. contandriopouli Quézel, $4x = 32$

V. densiflora Ledeb., $2x = 16$

V. erinoides Boiss. & Spruner, $2x = 16$

V. fruticans Jacq. subsp. *fruticans*, $2x = 16$

V. fruticans subsp. *cantabrica* M. Laínz, $2x = 16$

V. fruticulosa L., $2x = 16$

V. kellereri Degen & Urum., $2x = 16$

V. mampodrensis Losa & P. Monts., $2x = 16$

V. nummularia Gouan, $2x = 16$

V. saturejoides Vis., $2x = 16$

V. thessalica Benth., $2x = 16$

Species not investigated: *Veronica cachemirica* Gand., *V. capitata* Royle ex Benth., *V. chinoalpina* T. Yamaz., *V. daghestanica* Trautv., *V. emodi* T. Yamaz., *V. eriogyne* H. J. P. Winkl., *V. fedtschenkoi* Boriss., *V. filipes* P. C. Tsoong, *V. gorbunovii* Gontsch., *V. himalensis* D. Don, *V. kotschyana* Benth., *V. lanosa* Royle ex Benth., *V. lanuginosa* Benth., *V. luetkeana* Rupr., *V. macrostemon* Bunge ex Ledeb., *V. macrostemonoides* Zakirov, *V. mexicana* S. Watson, *V. monticola* Trautv., *V. quezelii* M. A. Fisch., *V. rockii* H.-L. Li, *V. ruprechtii* Lipsky, *V. serpylloides* Regel, *V. tianschanica* Linez.

VIII. *Veronica* subg. *Pocilla* (Dumort.) M. M. Mart. Ort., Albach & M. A. Fisch.

Species not investigated: *Veronica amoena* Steven ex M. Bieb., *V. violifolia* Hochst. ex Benth.

1. *Veronica* sect. *Subracemosae* (Benth.) Assejeva

1a. *Veronica* subsect. *Subracemosae* Benth.

$x = 7$

V. arguteserrata Regel & Schmalh., $6x = 42$

V. biloba L., $4x = 28$

V. campylopoda Boiss., $4x, 6x, 8x = 28, 42, 56$

V. capillipes Nevski, $4x = 28$

V. arguteserrata $\times$ *V. campylopoda*, $6x = 42$

Species not investigated: *V. bucharica* B. Fedtsch., *V. nevskii* Boriss., *V. ramosissima* Boriss., *V. stylophora* Popov ex Vved., *V. tenuissima* Boriss.

1b. *Veronica* subsect. *Cardiocarpae* Boriss. ex Elenevsky

$x = 7$ or $8?$

V. cardiocarpa (Kar. & Kir.) Walp., $2x = 14, 16$

Species not investigated: *Veronica intercedens* Bornm.

1c. *Veronica* subsect. *Brevistylae* Elenevsky

$x = 7$

V. rubrifolia subsp. *respectatissima* M. A. Fisch., $4x = 28$

Species not investigated: *Veronica avromanica* M. A. Fisch., *V. ferganica* Popov, *V. macropoda* Boiss., *V. viscosa* Boiss.

2. *Veronica* sect. *Pocilla* Dumort.

2a. *Veronica* subsect. *Agrestes* Benth.

$x = 7$

V. agrestis L., $4x = 28$

V. ceratocarpa C. A. Mey., $2x = 14$

V. filiformis Sm., $2x = 14$

V. francispetae M. A. Fisch., $2x = 14$

V. opaca Fr., $4x = 28$

V. persica Poir., $4x = 28$

V. polita Fr., $2x = 14$

V. siaretensis E. B. J. Lehm., $2x = 14$

Species not investigated: *Veronica bungei* Boiss., *V. longipedicellata* Saeidi.

IX. *Veronica* subgen. *Pentasepalae* (Benth.) M. M. Mart. Ort., Albach & M. A. Fisch.

Incertae sedis

Species not investigated: *Veronica aucheri* Boiss., *V. chionantha* Bornm., *V. czerniakowskiana* Monjuschko, *V. gaubae* Bornm., *V. khorassanica* Czerniak., *V. kopetdaghensis* B. Fedtsch., *V. minuta* C. A. Mey., *V. mirabilis* Wendelbo, *V. paederotae* Boiss.

1a. *Veronica* subsect. *Pentasepalae* Benth.

$x = 8$

V. aragonensis Stroh, $4x = 32$

V. austriaca L., $6x, 8x = 48, 64$

V. austriaca subsp. *dostalii* (Domin) Dostal, $6x = 48$

V. crinita Kit. ex Schult., $2x = 16$

V. jacquinii Baumg., $2x, 6x, 8x, 10x = 16, 48, 64, 80$

V. jacquinii subsp. *neicefii* Degen, $4x = 32$

V. kindlii Adamović, $2x = 16$

V. krylorii Schischk., $2x = 16$

V. orbiculata A. Kern, $4x = 32$

V. orsiniana Ten., $2x = 16$

V. prostrata L. subsp. *prostrata*, $2x = 16$

V. prostrata subsp. *sibirica* Watzl, $2x = 16$

V. rhodopea (Velen.) Degen ex Stoj. & Stef., $2x = 16$

V. rosea Desf., $2x = 16$

V. scheererii (J. P. Brandt) Holub, $4x = 32$

V. sennenii (Pau) M. M. Mart. Ort. & E. Rico, $8x = 64$

V. tenuifolia Asso subsp. *tenuifolia*, $2x = 16$

V. tenuifolia subsp. *fontqueri* (Pau) M. M. Mart. Ort. & E. Rico, $2x = 16$

V. tenuifolia subsp. *javalambrensis* (Pau) Molero & A. Pujadas, $2x, 4x = 16, 32$

V. teucrium L., $6x, 8x = 48, 64$

V. turrilliana Stoj. & Stef., $2x = 16$

Veronica $\times$ *gundisalvi* Sennen, $2x = 16$

1b. *Veronica* subsect. *Armeno-persicae* Stroh

$x = 8$

V. armena Boiss. & Huet., $2x = 16$

V. farinosa Hausskn., 2*x* = 16
V. microcarpa Boiss., 4*x* = 32

Species not investigated: *Veronica acrotheca* Bornm. & Gauba, *V. euphrasiifolia* Link, *V. liwanensis* K. Koch, *V. montbretii*, M. A. Fisch., *V. oltensis* Woronow.

- 1c. *Veronica* subsect. *Orientales* (Wulff) Stroh
x = 8
V. bombycina Boiss. & Kotschy, 2*x* = 16
V. caespitosa Boiss., 2*x* = 16
V. cinerea Boiss. & Bal., 2*x* = 16
V. cuneifolia D. Don, 2*x* = 16
V. dichrus Schott & Kotschy, 2*x* = 16
V. elmaliensis M. A. Fisch., 8*x* = 64
V. kurdica Benth., 6*x* = 48
V. macrostachya subsp. *sorgerae* M. A. Fisch., 2*x* = 16
V. multifida L., 2*x*, 4*x*, 6*x*, 10*x* = 16, 32, 48, 80
V. multifida × *V. dichrus*, 8*x* = 64
V. orientalis Mill., 4*x*, 8*x* = 32, 64
V. pectinata L., 2*x* = 16
V. thymifolia Sibth. & Sm., 2*x* = 16

Species not investigated: *Veronica allahuekberensis* Öztürk, *V. antalyensis* M. A. Fisch., Erik & Sümbül, *V. cetikiana* Öztürk, *V. fragilis* Boiss. & Hausskn., *V. fridericae* M. A. Fisch., *V. fuhsii* Freyn & Sint., *V. galathica* Boiss., *V. leiocarpa* Boiss., *V. polifolia* Benth., *V. polium* P. H. Davis, *V. rechingeri* M. A. Fisch., *V. surculosa* Boiss. & Balansa, *V. taurica* Willd., *V. tauricola* Bornm., *V. thymoides* P. H. Davis.

- 1d. *Veronica* subsect. *Petraea* Benth.
x = 8
V. peduncularis M. Bieb., 2*x* = 16

Species not investigated: *Veronica baranetskii* Bordz., *V. bogosensis* Tumadz., *V. borisovae* Holub, *V. caucasica* M. Bieb., *V. filifolia* Lipsky, *V. petraea* (M. Bieb.) Steven, *V. umbrosa* M. Bieb., *V. vendetta-deae* Albach.

X. *Veronica* subg. *Chamaedrys* (W. D. J. Koch) Buchenau

1. *Veronica* sect. *Alsinebe* Griseb.
1a. *Veronica* subsect. *Microspermae* (Römpf) Stroh
x = 8
V. arvensis L., 2*x* = 16

Species not investigated: *Veronica sartoriana* Boiss. & Heldr.

- 1b. *Veronica* subsect. *Microspermoides* Albach
x = 8
V. brevistyla Moris, 2*x* = 16

V. dillenii Crantz, 2*x* = 16
V. verna L., 2*x* = 16

2. *Veronica* sect. *Chamaedrys* W. D. J. Koch

- 2a. *Veronica* subsect. *Asiachamaedrys* Albach
x = 7?, ?
V. laxa Benth., 4*x*, ?*x* = 32, 46
V. magna M. A. Fisch., 6*x* = 42

- 2b. *Veronica* subsect. *Multiflorae* Benth.
x = 8
V. chamaedryoides Bory & Chaub., 2*x* = 16
V. chamaedrys L. subsp. *chamaedrys*, 2*x*, 4*x* = 16, 32
V. chamaedrys subsp. *micans* M. A. Fisch., 2*x* = 16
V. krumovii (Peev) Peev, 2*x* = 16
V. micrantha Hoffmanns. & Link, 2*x* = 16
V. orbelica (D. Peev) D. Peev, 2*x* = 16
V. vindobonensis (M. A. Fisch.) M. A. Fisch., 2*x* = 16

XI. *Veronica* subgen. *Pseudoveronica* J. B. Armstr.

1. *Veronica* sect. *Detzneria* (Schltr. ex Diels) Albach
x = ?
V. tubata (Diels) Albach, 6*x* = 38–42 or 48

2. *Veronica* sect. *Derwentia* (Raf.) B. G. Briggs
*x*_{Hebe} = 19, 20, 21
24 species, see Briggs and Ehrendorfer (2006) for review.

3. *Veronica* sect. *Hebe* (Juss.) Benth.
*x*_{Hebe} = 20, 21
For 121 species from New Zealand and adjacent islands, see Bayly and Kellow (2006) and Garnock-Jones and Lloyd (2004) for a review.

Species from New Guinea:

- V. albiflora* (Pennell) Albach, 2 *x*_{Hebe} = 12
V. ionantha Albach, 2 *x*_{Hebe} = 40

Species not investigated: *Veronica brassii* (Pennell) Albach, *V. carminea* Albach, *V. carstensensis* Wernham, *V. diosmoides* Schltr., *V. inflexa* Albach, *V. papuana* (P. Royen & Ehrend.) Albach, *V. strigosa* Albach, *V. randewateri* Wernham, *V. wilhelminensis* Albach.

XII. *Veronica* subg. *Triangulicapsula* M. M. Mart. Ort., Albach & M. A. Fisch.

- x* = 6
V. chamaepithyoides Lam., 4*x* = 24
V. grisebachii Walters, 2*x* = 12
Incertae Sedis within *Veronica*
x = 8
V. javanica Blume, 2*x* = 16